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Az iskolavezető jóváhagyása

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# 1 ELŐZMÉNYEK ÉS CÉLKITŰZÉSEK

## 1.1 Összefüggések az agrárélőhelyek térszerkezete és ökoszisztéma szolgáltatásokat nyújtó rovarközösségek között

Az utóbbi évtizedekben a mezőgazdasági területek egyre intenzívebb művelése és egyre nagyobb, a természetes élőhelyek kárára történő térnyerése miatt a természetes tájszerkezet világszerte sok helyütt drasztikusan megváltozott. Ennek a folyamatnak az eredményeként a rovarközösségek abundanciája és diverzitása is sok helyen erősen lecsökkent (lásd például HALLMANN et al. 2021; SÁNCHEZ-BAYO & WYCKHUYS 2021; WAGNER et al. 2021). Azonban egy egyedszámban erős és fajgazdag rovarközösség jelenléte rendkívül fontos az ökoszisztémák működéséhez, mivel sok rovarfaj jelentős, gyakran kulcsszerepet tölt be az életközösségekben belül. Az ökoszisztémák működésének fenntartása azért is fontos, mert csak ilyen módon maradnak azok az ember számára is hasznos szolgáltatások (= ökoszisztéma szolgáltatások) elérhetőek, amelyeket bizonyos rovarfajok illetve rovarcsoportok nyújtanak. Ezek a szolgáltatások különösen a mezőgazdasági, haszonnövényektől származó termények és termékek előállításához, valamint a minőségük megőrzéséhez szükségesek (ALTIERI 1999). Két közismert példa effajta rovarok által nyújtott szolgáltatásokra a ragadozó és parazitoid rovarok kártevő-gyérítő tevékenysége, vagyis a haszonnövények biológiai védelme természetes ellenségek által (JONSSON et al. 2014; BENGTSSON 2015), valamint a (vad) méhek és más rovarok megporzó tevékenysége (MELATHOPOULOS et al. 2015; FIJEN et al. 2018). Néhány rovarcsoport (például a zengőlegyek) képes mindkét szolgáltatást egyszerre nyújtani (DUNN et al. 2020).

Az életközösségekben betöltött fontos szerepük mellett sok rovarfaj érzékenyen reagál a természetes tájszerkezet megváltozására, ezért kifejezetten alkalmasak az ilyenfajta hatások felderítésére és nyomon követésére. Az utóbbi évtizedekben több olyan tanulmány készült, amely az agrártájban található különböző tájelemek, elsősorban a féltermészetes élőhelyek összetételének és elrendezésének különféle ökoszisztéma szolgáltatásokat nyújtó rovarfajokra illetve rovarcsoportokra kifejtett hatásait vizsgálták. Ezeknek a tanulmányoknak az eredményei azonban korántsem egyértelműek. Például egy szójabab (*Glycine max*) táblákban végzett kísérletben (MITCHELL et al. 2014) kimutatták, hogy bonyolultabb szerkezetű, azaz kisebb és keskenyebb táblákkal rendelkező tájegységekben nem csak a ragadozó rovarfajok diverzitása és abundanciája, hanem a levéltetvek egyedszáma is szignifikánsan magasabb volt. Egy másik tanulmány (ZIOŁKOWSKA et al. 2021) eredményei, amely keretében rovarölő-szereknek és a tájszerkezetnek – pontosabban a vizsgált táblákat szegélyező mezsgyék számának – a

*Bembidion lampros* futóbogárfajra kifejtett hatásait vizsgálta, azt mutatták, hogy a rovarölőszerek letális hatásának csökkentése sokkal erősebb hatással volt a faj egyedsűrűségének növekedésére mint (csak) a mezsgyék számának növelése. Egy Etiópiában végzett tanulmány (KEBEDE et al. 2018) eredményei, amely a tájszerkezetnek a *Busseola fusca* kukorica-kártevő bagolylepkefaj természetes ellenségeire kifejtett hatásait vizsgálta, viszont azt mutatták, hogy egy komplexebb tájszerkezet nagyobb kiterjedésű sövényekkel pozitív hatással volt a ragadozó természetes ellenségek abundanciájára, míg a parazitoid természetes ellenségek egyedszámára nem volt semmiféle hatással.

Az agrártáj szerkezete és különböző, rovarmegporzókkal kapcsolatos paraméterek közötti összefüggéseket szintén már néhány tanulmány keretében vizsgálták. Például egy intenzíven művelt Németországi agrártájban végzett tanulmány (JAUKER et al. 2009) eredményei azt mutatták, hogy míg a vadméhek egyedszáma a féltermészetes élőhelyektől való távolság függvényében csökkent, addig a zengőlegyek száma nőtt. Továbbá a vadméhek fajdiverzitása csak akkor csökkent a féltermészetes élőhelyektől való távolság függvényében, ha felvételezési transzektet körülvéő tájban a gyepek részaránya meglehetősen alacsony (<10%) volt. Egy másik tanulmány keretében (PFISTER et al. 2018), amelyet oriástök (*Cucurbita maxima*) táblákban végeztek, a vizsgálatot végző kutatók azt találták, hogy a poszméhek (*Bombus* spp.) viráglátogatási gyakorisága a növekvő mezőgazdasági területek részarányának függvényében szignifikánsan csökkent. Azonban a táblák közvetlen szomszédságában található féltermészetes élőhelyek jelenlétének semmiféle hatását nem sikerült kimutatniuk.

Összegezve kijelenthető, hogy ezek és más hasonló tanulmányok eredményei ellenére még mindig meglehetősen keveset tudunk az agrártáj térszerkezete és a mezőgazdasággal kapcsolatos ökoszisztéma szolgáltatásokat nyújtó rovarfajok, illetve –csoportok közötti összefüggésekről.

## **1.2 A tájszerkezet felmérése**

A tájökológia tudományágának kezdeti elméleti alapjait a német biogeográfus, Carl Troll fektette le közvetlenül a Második Világháború előtti években, és maga a “tájökológia” (ném. “Landschaftsökologie”) kifejezés is tőle származik (TROLL 1971). Ehhez segítségére volt az akkortájt erősen fejlődő légi fényképezés technikája és az ökoszisztémák működésének kutatása (CUSHMAN et al. 2010a; KUPFER 2011). A tájökológia elsősorban egy vizsgált tájegység térszerkezetének, és az itt zajló ökológiai folyamatok közötti kölcsönhatásokat

vizsgálja (TURNER 1989; WIENS 2002). A modern számítástechnika, valamint a manapság könnyen és nagy számban elérhető, magas felbontású műholdképek nagyban segítik ezeknek az összefüggéseknek a felderítését (CUSHMAN et al. 2010a).

A tájökológiában a tájszerkezetet – vagyis egy vizsgált tájegységben található tájelemek összetételét, egymáshoz való térbeli viszonyát és szerkezetét – úgynevezett tájmetriai mutatók segítségével számszerűsítjük. Az ember által kevésbé bolygatott, a természetes állapothoz közeli tájszerkezetet “elsődleges” tájszerkezetnek is szokták nevezni, míg a “másodlagos” tájszerkezet egy, az emberi beavatkozások eredményeként az eredeti állapottól jelentősen eltérő tájszerkezet. Ha a “másodlagos” tájszerkezet évszázadok vagy évezredek óta tartó természeti hatások és hagyományos, környezetkímélő emberi tevékenység együttes eredménye, akkor azt “kultúrtáj”-ként is szokták emlegetni (WALZ & SYRBE 2013).

A tájszerkezet tudományos jellegű felmérése a második világháború utáni időszakban vette kezdetét, eleinte az “elsődleges” tájszerkezetre fókuszálva (MEZŐSI & FEJES 2004). Később azonban, főleg az 1980-as évektől kezdődően, a kutatások egyre inkább a tájszerkezetbe való emberi beavatkozások ökoszisztémákra kifejtett hatását vizsgálták (MEZŐSI & FEJES 2004). A tájszerkezet felmérésére az úgynevezett “folt-folyosó-mátrix” modell lett kifejlesztve (FORMAN & GODRON 1986; FORMAN 1995), amely a MacArthur és Wilson féle szigetbiogeográfia-elméleten alapszik (MACARTHUR & WILSON 1967). Ez a modell az alakjuk alapján három különféle tájelemet különböztet meg, amely egy vizsgált tájegységben előfordulhat (FORMAN & GODRON 1986; FORMAN 1995):

- a) Foltok: Nem-lineáris, viszonylag homogén és a környezetüktől eltérő területi egységek.
- b) Folyosók: Lineáris, vagyis hosszúka és sávszerű területi egységek, amelyek a környezetüktől eltérnek és általában foltokat kötnek össze. A folyosók érintkezhetnek a foltokkal, de térbeli távolság is lehet a tájelemek között. A foltokkal azonos vagy eltérő típusúak lehetnek.
- c) Mátrix: A legnagyobb térbeli kiterjedésű folt egy vizsgált tájegységben, amelybe a többi, eltérő típusú tájelem be van ágyazódva.

Olyan tájmodellek, amelyek a szigetbiogeográfia-elméletre vannak alapozva, általában csak egyetlen egy folt típust vizsgálnak. A mátrixra úgy tekintenek, mint egy, a vizsgált organizmus szempontjából ökológiailag ellenséges vagy semleges háttérre, amelyben a foltok és folyosók, mint szigetek egy tengerben helyezkednek el (CUSHMAN et al. 2010b). Ezzel a meglehetősen statikus modellel szemben létezik egy másik szemléletmód is, az úgynevezett “táj-mozaik

modell” (WIENS et al. 1993; WIENS 1995). Ez az elmélet vagy modell elveti a foltok és a mátrix szigorú megkülönböztetését, és a vizsgált tájat egy térben és időben folyamatosan változó, dinamikus és heterogén entitásként kezeli, amely számos különböző folt típus mozaikjából áll (CUSHMAN et al. 2010b).

A tájszerkezet vizsgálatára számos különféle tájmetriai mutatót fejlesztettek ki, amelyek a vizsgált tájegységben található foltok részarányát, térszerkezetét és diszpergáltságát (= térbeli szét daraboltságát) számszerűsítik (lásd például LI & REYNOLDS 1993; MCGARIGAL & MARKS 1995; JAEGER 2000). Egy tájelemzésnél alapvetően nem teszünk különbséget foltok és folyosók között (BOGAERT et al. 2014). Ha esetleg a vizsgálat szempontjából mégis szükséges lineáris és nem-lineáris tájelemek között különbséget tenni, akkor ezeket előzetesen külön kategóriákba kell sorolni. Mivel a mátrix általában a legdominánsabb folt a vizsgált tájegységben, ezért ki szokták hagyni a tájelemzésből. Abban az esetben viszont, ha a mátrix nem mint ‘valódi’ háttér viselkedik, és a többi folthoz vagy folt típushoz képest nem annyira domináns, akkor foltként szokták kezelni, és a tájelemzésbe is be szokták vonni.

A tájszerkezet elemzéséhez és számszerűsítéséhez legszélesebb körben használt szoftver a McGarigal és Marks (MCGARIGAL & MARKS 1995) által kifejlesztett FRAGSTATS program. Ez a szoftver raster adatokat használ az egy vizsgált tájegységben előforduló térbeli mintázatok felméréséhez és elemzéséhez, vagyis a tájelemzéshez. Egy ilyen tájelemzést alapvetően három heterogenitási szinten lehet elvégezni:

1. Folt szinten, ha egyéni foltok térbeli tulajdonságait vizsgáljuk.
2. Osztály szinten, ha az összes azonos típusú folt térbeli tulajdonságait vizsgáljuk.
3. Táji szinten, ha az összes, egy vizsgált tájegységben található folt térbeli tulajdonságait kívánjuk számszerűsíteni.

Annak ellenére, hogy számos különféle tájmetriai mutató létezik, alapvetően mindegyik vagy a vizsgált tájegységben található tájelemek összetételét, vagy térbeli elrendezését, vagy néhány esetben mindkettőt egyszerre írja le. Továbbá, mivel a legtöbb tájmetriai mutató kiszámítása tájfoltok ugyanazon geometriai tulajdonságain, mint például a területükön vagy kerületükön alapszik, ezért a legtöbbjük között magas a korreláció. Vagyis gyakorlatilag a vizsgált tájnak ugyanazon térbeli tulajdonságait írják le, ami legtöbbjüket redundánssá, azaz feleslegessé teszi. Ezidáig számos kísérlet történt a redundáns mutatók megtalálására és kiszűrésére (például LI & REYNOLDS 1995; MCGARIGAL & MCCOMB 1995; RIITERS et al. 1995; CUSHMAN et al. 2008). Ezeknek a tanulmányoknak eredményei azt mutatták, hogy a mutatók többsége



tényleg erősen korrelál egymással, és hogy általában néhány belőlük elegendő, hogy a vizsgált tájegységről egy messzemenően pontos leírást kapjunk. Azonban az eredmények arra is engednek következtetni, hogy a mutatók közötti korreláció erősen függ magától a vizsgált tájegység mintázatától, és hogy nem létezik egy előre lehatárolható, minden esetben alkalmazható készlet tájmetriai mutatókból. Ezért a mutatók kiválasztása elsősorban a tudományos kérdésfeltevéstől függ.

Végezetül még ki szeretném emelni a tájelemzéshez választott térbeli lépték fontosságát. A térbeli lépték egy raster-kép formájában vizsgált tájegység esetében két fő részből áll: egyrészt a térbeli kiterjedéséből, illetve méretéből, másrészt az elemzett raster-kép térbeli felbontásából, illetve pixel-méretéből (FORMAN & GODRON 1986; TURNER et al. 1989; WIENS 1989). Ezeknek a paramétereknek előzetes beállítása, illetve kiválasztása jelentősen befolyásolja a kiszámított tájmetriai mutatók értékeit és így a tájelemzés eredményeit. A lépték két térbeli komponense mellett még létezik egy harmadik, nem-térbeli komponens is, amelyet nem szabad figyelmen kívül hagyni: a tematikus felbontás, vagyis a vizsgált tájegységben található folt típusok száma. Ez a paraméter is jelentős hatással lehet a tájelemzés eredményeire. Általában minél finomabb a tematikus felbontás, annál precízebb képet kapunk a vizsgált ökológiai jelenségekről vagy folyamatokról, de annál bonyolultabbá és egyre nehezebben kivitelezhetővé válik maga az elemzés.

### **1.3 Az értekezés főbb célkitűzései**

Az értekezés keretében bemutatott mindhárom tanulmánynak a fő célkitűzései közé tartozott a kísérleti helyszíneket körülvevő agrártáj szerkezetének különböző rovarfajokkal, illetve rovarcsoportokkal kapcsolatos paraméterekre kifejtett hatásainak felmérése. A tájszerkezet felméréséhez az előző fejezetben említett FRAGSTATS program által kiszámított tájmetriai mutatókat használtam. Az első két tanulmány terepi felvételezései Magyarország intenzív mezőgazdasági területek által dominált középső részén folytak, ahol a féltermészetes élőhelyek részaránya igen alacsony. Ezzel szemben a harmadik tanulmány terepi felvételezései egy alacsony intenzitású agrártájban, Románia középső részén (vagyis Erdélyben, Székelyföldön) zajlottak. Itt a féltermészetes vagy természetes élőhelyek (úgy mint virágfajokban gazdag rétek, mezők, illetve erdők) és a mezőgazdasági területek sokkal kiegyensúlyozottabb részarányaival találkozunk a tájban. A tájszerkezeti hatások felderítése mellett az előző fejezetben megtárgyalt néhány, tájmetriai mutatókkal kapcsolatos módszertani kérdés kivizsgálása is szerepelt az első

két tanulmány célkitűzései között. Például az első tanulmány keretében a redundáns mutatók megtalálására és kiszűrésére – vagyis, hogy megtaláljam a legnagyobb magyarázó erővel bíró tájmetriai mutatókat – egy, újfajta elemekkel rendelkező szelekciós procedúrát alkalmaztam, illetve vizsgáltam. Továbbá, az első két tanulmány esetében a változó térbeli lépték hatásait is vizsgáltam. Ennek a három tanulmánynak tudományos cikkek formájában leközölt szövegei a mellékletében találhatóak. A három tanulmánynak főbb koncepcióit és célkitűzéseit a következő három alfejezetben mutatom be.

### *1.3.1 Az első tanulmány koncepciói és célkitűzései*

A veresnyakú árpabogár (*Oulema melanopus*) lárvái a gabonafélék, különösen az őszi búza (*Triticum aestivum*) egyik fontos kártevője (HAYNES & GAGE, 1981). Mind maga az árpabogár (CASAGRANDE et al. 1977; PHILIPS et al. 2012), mind sok kártevő természetes ellenségei (lásd például TAKÁCS & FRANK 2009) fás területekhez kötődnek, amelyeket vagy átmeneti (például az árpabogár esetében telelő), vagy állandó élőhelyként használnak. Az intenzív mezőgazdasági területek által dominált közép-magyarországi térségben, ahol ez a tanulmány folyt, alapvetően kétféle fás területtel lehet találkozni: egyrészt lineáris elemekkel mint erdősávokkal vagy fasorokkal, amelyek általában fajgazdag aljnövényzettel rendelkeznek (TAKÁCS & FRANK 2009), másrészt nyarasok (*Populus tremula*) vagy akácok (*Robinia pseudoacacia*) terjedelmes ültetvényeivel, amelyek viszont általában erősen zárt lombkoronával és fajszegény aljnövényzettel rendelkeznek (WEIH et al. 2003; VÍTKOVÁ et al. 2017). Az első tanulmány fő célja az volt, hogy a természetes ellenségek által a veresnyakú árpabogár lárváira kifejtett gyérítő hatást számszerűsítsük búzatáblák közelében található két különböző térszerkezetű fás terület hatásainak függvényében. Ennek érdekében a lárvák által okozott levélfelületvesztést vizsgáltuk kizárásos kísérletekkel.

### *1.3.2 A második tanulmány koncepciói és célkitűzései*

A napraforgó (*Helianthus annuus*) az Európai Unióban (= EU-28) a repce után a második legfontosabb olajnövény, amit több mint 4 millió hektáron termesztnek (EUROSTAT 2018). Magyarországon a napraforgó a legfontosabb olajnövény, amit több mint fél millió hektáron termesztnek 2005 óta (KSH 2019). Annak ellenére, hogy a napraforgó képes az önbeporzásra, a rovarmegporzók általi idegenbeporzás gyakran több és jobb minőségű terméshez vezet

(HEVIA et al. 2016; TERZIĆ et al. 2017; SILVA et al. 2018), akár táblánként 40 százalékkal (PERROT et al. 2019). Világszerte a háziméh (*Apis mellifera*) a napraforgó első számú megporzója (lásd például GREENLEAF & KREMEN 2006; NDERITU et al. 2008; CERRUTTI & PONTET 2016; MARTIN & FARINA 2016). Azonban a vadméhek megporzói tevékenysége is kimutathatóan képes növelni a napraforgó terméshozamát. A saját beporzási tevékenységük mellett, jelenlétükkel több mozgásra kényszerítik a háziméheket, így növelve azok beporzási hatékonyságát (GREENLEAF & KREMEN 2006; CARVALHEIRO et al. 2011; SARDIÑAS & KREMEN 2015). Nagyon úgy tűnik, hogy ez a mozgásra ösztönző hatás elsősorban hibrid napraforgó fajták beporzásánál játszik fontos szerepet, ahol az anyanövények hímsterilek, és csak egy másik, hímfertilis napraforgótól képesek beporzódni (GREENLEAF & KREMEN 2006; OZ et al. 2009; MARTIN & FARINA 2016). Ezért a napraforgó sikeres termesztéséhez fontos tudni, hogy a táblákat körülvevő tájban található tájelemek összetétele és elrendezése hogyan hat a vad rovarmegporzók egyedszámára és fajgazdagságára. Azonban a napraforgó vad rovarmegporzóira kifejtett tájszerkezeti hatásokat ezidáig csak néhány tanulmány keretében vizsgálták. Ezeknek a tanulmányoknak az eredményei arra utalnak, hogy a féltermészetes élőhelyek magasabb száma a napraforgótáblák körül pozitívan hat a vad rovarmegporzók egyedszámára és fajgazdagságára (BENNETT & ISAACS 2014; RIEDINGER et al. 2014; BIHALY et al. 2018). Azonban a napraforgótáblákat körülvevő tájban található különböző tájelemek összetételének és elrendezésének, vagyis bonyolultabb tájszerkezeti paramétereknek a hatásait ezidáig egy tanulmány keretében sem vizsgálták. Az itt bemutatott második tanulmány pont ennek a hiánynak a pótlását tűzte ki célul, méghozzá a vizsgált napraforgótáblákat körülvevő táj térszerkezeti paramétereinek felmérését, valamint ezeknek a paraméternek a napraforgó viráglátogatási gyakoriságára kifejtett hatásainak felderítését.

### *1.3.3 A harmadik tanulmány koncepciói és célkitűzései*

Fészekcsapdák segítségével nemcsak az üregekben fészkelő hártvásszárnyúak egyedszámát, diverzitását és trofikus kapcsolatait lehet vizsgálni, hanem erre az élőlénycsoportra kifejtett tájszerkezeti hatások felderítésére is kifejezetten alkalmas a fészekcsapdás adatgyűjtés módszere (lásd például STECKEL et al., 2014; STANGLER et al., 2015; STAAB et al., 2018; MAYR et al., 2020). A növekvő mezőgazdasági intenzifikáció és urbanizáció eredményeként, főleg a sűrűn lakott régiókban, mint például Nyugat-Európában, számos rovarfaj élőhelyének területe vagy lecsökkent, vagy szétdarabolódott, ami világszerte sok helyen visszaesést okozott

a rovarok egyedszámában és fajgazdagságában (lásd például PIANO et al. 2020; WAGNER 2020; RAVEN & WAGNER 2021; SÁNCHEZ-BAYO & WYCKHUYS 2021). Ezért minden további adat és információ üregekben fészkelő hártvászárnyúakról, és az ezeket befolyásoló tájszerkezeti hatásokról segítséget nyújthat, hogy az érdeklükben elvégzett védelmi intézkedések sikerrel járjanak. Az eddigi nyugat-európai tanulmányok többsége, amely üregekben fészkelő hártvászárnyúakkal foglalkozott, intenzív mezőgazdasági területeken folyt (lásd például HOLZSCHUH et al. 2009 és 2010; FABIAN et al. 2013 és 2014). Ezzel szemben olyan nyugat-európai tanulmányok, amelyek ugyanezt alacsony intenzitású mezőgazdasági területeken vagy természetközeli élőhelyeken vizsgálták sokkal ritkábbak (lásd például ALBRECHT et al. 2007; SOBEK et al. 2009; KREWENKA et al. 2011). Továbbá Kelet-Európa nagy részén üregekben fészkelő hártvászárnyúakat, néhány tanulmánytól eltekintve (például BUDRYS et al. 2010; BIHALY et al. 2021), még egyáltalán nem vizsgáltak. Ezért a harmadik tanulmány keretében fészekcspadás vizsgálatokat végeztünk Románia ember által kevésbé befolyásolt és természetközeli területekben gazdag központi részén. A tanulmány konkrét célja az üregekben fészkelő hártvászárnyúak abundanciájának és diverzitásának, valamint ezek közül a ragadozó csoportok pókzsákmány-preferenciájának felmérésére volt, a kísérleti helyszíneket körülvevő alacsony intenzitású mezőgazdasági területek részaránya és szegélysűrűsége függvényében.

## 2 ANYAGOK ÉS MÓDSZEREK

### 2.1 Első tanulmány: Lineáris fás tájelemek segítségével enyhíthető a veresnyakú árpabogár által okozott levélfelületveszteség

A szabadtéri kísérletek két éven keresztül (2014 és 2015-ben) a Nagyalföld északnyugati részén, a Jászságban zajlottak. Mindkét évben 17 búzatábla lett a kísérletek helyszínéül kiválasztva. 2014-ben a táblaszegélyre merőlegesen négy sor búzanövényt, mint transzektet jelöltünk ki. Mind a négy transzekt mentén 2-25-50-75 m távolságra a szegélytől, négy-négy darab búzanövényt választottunk ki. Növényenként öt darab, előzetesen összegyűjtött hím és nőstény árpabogár imágót (összesen 2380 egyed) helyeztünk ki, és a kísérleti növényeket ezután egy acélvázalattal támogatott izolátorhálóval letakartuk. Néhány nappal később, miután a nőstények lepetéztek, az imágók el lettek távolítva. Ezt követően az izolátorhálókat a negyedik sor kivételével (= "zárt" kezelés), nem helyeztük vissza (= "nyitott" kezelés), így a növények hozzáférhetővé váltak a természetes ellenségek számára. A 2015-ös szabadtéri kísérlet hasonlóan volt felépítve, mint a 2014-es, azzal a különbséggel, hogy ebben az évben csak három sor búzanövény lett transzektnek kijelölve, amelyek közül a középső sor volt a "zárt" és a két szélső sor a "nyitott" kezelés. Az árpabogár kártételét a levélfelületveszteséggel számszerűsítettük oly módon, hogy növényenként 10 darab levélre nézve a teljes levélfelülethez viszonyított károsított levélfelület arányát becsültük meg vizuálisan. A természetes ellenségek gyérítő hatása a "zárt" és "nyitott" kezelések közötti átlagos levélfelület-veszteségbeli különbségekből (=  $LSL_{DIFF}$ ) lett kiszámítva. A 34 búzatáblát körülvevő táj feltérképezése 500 m átmérőjű tájszektorokként a QGIS szoftverben történt, lineáris (= szélesebb erdősávok) és nem-lineáris (= monokultúras faültetvények) fás tájelemeket megkülönböztetve. Az így elkészített vektortérképek 8 térbeli léptékben (50 méteres lépésekben 150-500 m között) raszter-képekké lettek átalakítva. Ezekből a raszter-képekből a FRAGSTATS szoftver a kétféle fás tájelem 36 különféle tájmetriai mutatóját számította ki. Következő lépésként a tájmetriai mutatók magas számának csökkentésére egy két-lépcsős szelekciós procedúrát használtam, amely először a tájmetriai mutatók közötti korrelációk alapján a mutatók számát egy kezelhető mennyiségre lecsökkentette. Ezután a fennmaradó tájmetriai mutatók, mint magyarázó változók, valamint a gyök-transzformált  $LSL_{DIFF}$  értékei, mint függő változó lineáris modellekbe lettek integrálva, amelyekből automatizált modell-szelekciókat alkalmazva sikerült a legerősebb magyarázó erővel bíró tájmetriai mutatókat beazonosítani. Az egész szelekciós procedúra és minden más statisztikai elemzés az R statisztikai szoftverben történt.

## **2.2 Második tanulmány: A tájszerkezet hatással van a napraforgó rovarmegporzóinak viráglátogatási gyakoriságára**

A szabadtéri kísérletek, ugyanúgy, mint az első tanulmány esetében, a Jászság északnyugati részén, két éven keresztül (2014 és 2015-ben) évente 18 darab véletlenszerűen kiválasztott napraforgótáblában folytak. A kísérletek keretében a napraforgóvirágokat látogató megporzók megfigyelésére került sor. A megfigyelések nappal 9-17 óra között történtek. A megporzó rovarok megfigyelését és gyűjtését két, a táblaszegélyre merőlegesen futó transzekt mentén végeztük, amelyek 10 méterre helyezkedtek el egymástól. A megfigyelési és gyűjtési pontok 5-25-50-75 méterre voltak a táblaszegélytől. Minden pontnál kilenc napraforgófejen 10 percen keresztül figyeltük a megporzókat. A megfigyelések során három csoportban (háziméhek, vadméhek, egyéb megporzók) rögzítettük az egyedszámokat. A 36 napraforgótáblát körülvevő táj feltérképezése 750 m átmérőjű tájszektorokként a QGIS szoftverben történt, lágyszárú féltermészetes élőhelyeket, mint például gyepeket vagy mezsgyét, valamint az összes, a tájszektorok határain belül található napraforgótáblát megkülönböztetve. Lehetséges léptékhatások felderítésére a vektortérképek 13 léptékben (50 méteres lépésekben 150-750 m között) lettek raszter-képekké átalakítva. A kétféle vizsgált tájelem térbeli tulajdonságait a raszterképekből a FRAGSTATS szoftver segítségével a következő három tájmetriai mutató formájában számoltam ki: részarány ('Percentage of Landscape'), szegélysűrűség ('Edge Density') és diszpergáltság ('Dispersion Index'). Ez utóbbi tájmetriai mutató kiszámításához az 'Aggregációs Index' (amely a foltok aggregáltságát, illetve kompaktságát méri) értékeit mínusz eggyel szoroztam meg. Az összes statisztikai elemzést az R szoftverben végeztem. A kétféle tájelem térbeli tulajdonságainak a három megporzó csoport viráglátogatási gyakoriságára kifejtett hatásait Poisson eloszlású általánosított kevert hatású modellekkel (GLMM) vizsgáltam. Ehhez mindhárom tájmetriai mutató, a kétféle tájelemre külön bontva, mint magyarázó változó lett a Poisson GLMM-ekbe integrálva.

## **2.3 Harmadik tanulmány: Üregekben fészkelő hártványászárnyúak előzetes felmérése egy Erdélyben található alacsony intenzitású agrártájban**

A harmadik tanulmány vizsgálati helyszínei a Vargyas-szoros környékén, Hargita és Kovászna megyék (Székelyföld, Erdély, Románia) határán voltak. Az összesen nyolc kísérleti helyszín három völgyben, 530-630 méteres tengerszint feletti magasság között helyezkedett el. Ezek közül két helyszín az Északi Vargyas-völgyben, valamint három-három a Déli Vargyas-

völgyben és a Körös-völgyben volt található. Az Északi Vargyas-völgyben elsősorban extenzív legeltetés folyik és gyakoriak a rétek és kaszálók, míg a Déli Vargyas-völgy túlnyomó része, elzártsága miatt, erdők és fás területek által borított. A két völgyet a Vargyas-szoros választja el. A Vargyas-völgyekhez képest a Körös-völgyben sokkal erősebb az emberi hatás, és a déli részén szántók is találhatóak. Ezekből a tájhasználati intenzitásból tapasztalható különbségekből adódóan az alacsony intenzitású mezőgazdasági területek aránya a természetes erdőterülethez képest helyszínről helyszínre változó. Helyszínenként négy fészekcsapdát helyeztünk ki 2018 májusának végén. A fészekcsapdák 12 cm átmérőjű és 23 cm hosszúságú PVC csövekből álltak. A csöveket kb. 22 cm hosszú, elől-hátul nyitott nádszálakkal töltöttük meg. A csapdák összegyűjtése augusztus végén történt. Az összegyűjtött csapdákat először a szabadban, egy árnyékos, száraz helyen tároltuk, majd 2019 januárjában hűtőszekrénybe kerültek. Ezután megkezdődött a csapdák feldolgozása, vagyis a nádszálak felbontása és az adatok feljegyzése. Abban az esetben, ha egy nádszálban egy vagy több fészek volt, a következő adatok illetve paraméterek kerültek feljegyzésre: (a) a nádszál átmérője; (b) a költőkamrák száma, amelyekben vagy hártványásszárnyú ivadékok (lárvák vagy kokonok), vagy pókok voltak; (c) a fészekanyag típusa; (d) a lárvák vagy kokonok színe. A (c) és (d) paraméter alapján összesen hét fészektípust lehetett megkülönböztetni. Mind a hét fészektípus esetében legalább két darab nádszál, mint mintát, keltetésre műanyag zacskókba helyeztünk. Az imágók kikelése után közülük legalább két egyedet begyűjtöttünk és genusz szinten meghatároztunk. Összesen nyolc genuszt sikerült meghatározni: *Ancistrocerus*, *Auplopus*, *Dipogon*, *Hylaeus*, *Megachile*, *Osmia*, *Symmorphus*, és *Trypoxylon*. Az *Ancistrocerus* és *Symmorphus* genuszok esetében a fészektípust nem lehetett vizuálisan megkülönböztetni, ezért ennek a két genusznak a fészkeit egy közös csoportba, az Eumeninae (= fazekasdarazsak) alcsaládba soroltuk. A fészkekben talált pókzsákmányt család szinten meghatároztuk, és a három, pókokat ragadozó hártványásszárnyú csoporthoz (= *Auplopus*, *Dipogon* és *Trypoxylon*) rendeltük. A kísérleti helyszíneket körülvevő táj feltérképezése 250 m átmérőjű tájszektorok formájában a QGIS szoftver segítségével történt. A FRAGSTATS szoftverben egyetlen egy tájalelem-kategóriának két tájmetriai mutatóját, még hozzá a részarányát és szegélysűrűségét számítottam ki. Ez a tájalelem az 'alacsony intenzitású mezőgazdasági területek' elnevezésű tájalelem volt, amely réteket, kaszálókat és kis-parcellás mezőgazdasági területeket foglalt magába. Az alacsony intenzitású mezőgazdasági területek részaránya és szegélysűrűsége, és a hártványásszárnyúak költőkamráinak, valamint a fészkekben talált gyakoribb pókzsákmányok egyedszámai közötti kölcsönhatásokat Poisson eloszlású GLMM-ekkel, a vizsgált tájalelem részaránya és szegélysűrűsége és a hártványásszárnyúak valamint a *Trypoxylon* pókzsákmányának Shannon

Diverzitási Indexe közötti kölcsönhatásokat viszont lineáris modellekkel elemeztem. Az összes statisztikai elemzést az R szoftverben végeztem.

### **3 EREDMÉNYEK**

#### **3.1 Első tanulmány: Lineáris fás tájelemek segítségével enyhíthető a veresnyakú árpabogár által okozott levélfelületveszteség**

A veresnyakú árpabogár lárvái által okozott levélfelületveszteség az izolátorhálókkaal védett („zárt”) búzanövények esetében ( $= 64.9 \pm 35.7\%$ ) jóval magasabb volt, mint a védtelen („nyitott”) növényeknél ( $= 14.3 \pm 19.7\%$ ). Ez a különbség egy kétmintás Welch t-teszt szerint erősen szignifikáns volt ( $t = 15.542$ ,  $df = 168.05$ ,  $p$ -érték  $< 0.001$ ). A táblaszegélytől való távolságnak viszont lineáris modellek szerint sem a „nyitott”, sem a „zárt” kezelések esetében nem volt szignifikáns hatása.

Mindkét vizsgált fás tájelem szignifikáns, de ellentétes hatásokat mutatott az árpabogár kártételének enyhítésével kapcsolatban. A szelekcións procedúra segítségével sikerült tájmetriai mutatók számát a lineáris fás tájelemek esetében két, illetve a monokultúrás faültetvények esetében egy mutatóra lecsökkenteni. A lineáris fás tájelemek tájmetriai mutatói közül az ‘Aggregációs Index’, amely a vizsgált tájegységekben található foltok aggregáltságát, illetve kompaktságát méri, a vizsgált térbeli léptékek többségénél, valamint a szegéllysűrűség a vizsgált két legkisebb léptéknél (150-200 méternél) fejtett ki pozitív, szignifikáns hatásokat az árpabogár kártételének enyhítésére. Ezzel ellentétben a monokultúrás faültetvények növekvő részaránya szignifikánsan negatív hatásokat mutatott az árpabogár kártételének enyhítésére 200 és 500 m között, a legerősebben 250 méternél.

#### **3.2 Második tanulmány: A tájszerkezet hatással van a napraforgó rovarmegporzóinak viráglátogatási gyakoriságára**

A két vizsgálti év folyamán összesen 2993 (lehetséges) rovarmegporzót figyeltünk meg a napraforgófejekén. Az egyedek döntő többsége ( $= 85.2\%$ ) a házi méhek (*Apis mellifera*) közé tartozott. Ehhez képest a megfigyelt vad rovarmegporzók egyedszáma meglehetősen alacsony volt. Az összes megfigyelt rovarmegporzók közül a vadméhek csak 7.8%-ot ( $n = 233$ ) és a nem-méh rovarmegporzók csak 7.0%-ot ( $n = 209$ ) tettek ki.



A háziméhek viráglátogatási gyakoriságára, amelyek a leggyakoribb napraforgókat látogató megporzók voltak, a lágyszárú féltermészetes élőhelyek vizsgált tájszektoron belüli nagyobb részaránya és erősebb diszpergáltsága szignifikánsan pozitív hatásokat mutatott. Ezek a hatások 350 és 500 m között voltak a legerősebbek. A napraforgótáblák tájmetriai mutatói viszont nem fejtettek ki semmiféle szignifikáns hatást a háziméhek esetében. A háziméhekhez hasonlóan a vadméhek viráglátogatási gyakoriságára a lágyszárú féltermészetes élőhelyek tájszektoron belüli nagyobb részaránya és erősebb diszpergáltsága szintén szignifikánsan pozitív hatást gyakorolt. Ezek a hatások lépték-függők voltak, és míg a diszpergáltság esetében kisebb léptékeknél (150-300 méternél), addig a részarány esetében inkább nagyobb léptékeknél (550-750 méternél) voltak erősebbek. A vadméhek viráglátogatási gyakoriságára a napraforgótáblák szegélysűrűsége nagyobb léptékeknél (500-750 méternél) szignifikánsan negatív hatást gyakorolt. A nem-méh megporzók viráglátogatási gyakoriságára csak a lágyszárú féltermészetes élőhelyek erősebb diszpergáltsága gyakorolt szignifikánsan pozitív hatást. Ez a hatás lépték-függő volt és 450 méternél érte el a csúcsertékét. A napraforgótáblák egy tájmetriai mutatója sem hatott szignifikánsan a nem-méh megporzók viráglátogatási gyakoriságára.

### **3.3 Harmadik tanulmány: Üregekben fészkelő hártványászárnyúak előzetes felmérése egy Erdélyben található alacsony intenzitású agrártájban**

Összesen 990 hártványászárnyú fészket találtunk 4,857 nádszámban. A fészkek többségét ( $n = 888$ ) magányos darazsak építették. Ezek közül a legtöbb fészkek ( $n = 560$ ) a *Trypoxylon* genuszhoz tartozott. Ezt követte a *Dipogon* genusz 158 fészekkel, a fazekasdarázsok (Eumeninae alcsalád) 152 fészekkel, és az *Auplopus* genusz összesen 18 fészekkel. A magányos méhek által épített fészkek száma alacsonyabb volt ( $n = 102$ ). Ezek közül a *Hylaeus* genusz 61 fészket, az *Osmia* genusz 23 fészket és a *Megachile* genusz 18 fészket épített. Ami az azonosítható pókszákmanyt illeti, a *Trypoxylon* genusz összesen 1,471 darab, többségében keresztspókot (Araneidae;  $n = 1,118$ ), a *Dipogon* genusz 99 darab, többségében karolópókot (Thomisidae;  $n = 93$ ), és az *Auplopus* genusz egy darab kalitpókot (Clubionidae) zsákmanyt.

Az *Auplopus*, *Megachile* és *Osmia* hártványászárnyú genuszok költőkamráinak számai mind szignifikáns korrelációt mutattak a vizsgált helyszínek körül található alacsony intenzitású mezőgazdasági területek részarányával és szegélysűrűségével. A legerősebb hatásokat az *Osmia* magányos vadméh genusz esetében tudtuk kimutatni, ahol mind a részarány, mind a szegélysűrűség negatívan hatott a költőkamrák számára. Az *Auplopus* útonállódarázs

(Pompilidae) genusz esetében az alacsony intenzitású mezőgazdasági területek felemás hatásokat mutattak a költőkamrák számára: míg a szegélyesűrűségük szignifikánsan pozitívan hatott, addig a részarányuk negatívan. A *Megachile* magányos vadméh genusz esetében mindkét tájmetriai mutató hatása szignifikánsan pozitív volt. A póksákmány közül a *Dipogon* kaparódarázs genusz által zsákmányolt karolópókok (Thomisidae) számára negatívan hatott az alacsony intenzitású mezőgazdasági területek részaránya. A *Trypoxylon* kaparódarázs genusz által zsákmányolt pókok Shannon diverzitására viszont pozitívan hatott ugyanez a tájmetriai mutató.

#### 4 KÖVETKEZTETÉSEK ÉS JAVASLATOK

Ennek az értekezésnek a fő célkitűzése, ahogyan a címe is utal rá, tájszerkezeti hatások tájmetriai mutatók segítségével történő felderítése volt. Ezt három különböző tematikájú, rovarokkal kapcsolatos tanulmány keretében próbáltam demonstrálni. Mindhárom tanulmány esetében sikerült a tájszerkezet statisztikailag szignifikáns hatásait feltárni, annak ellenére, hogy a tanulmányok teljesen más tudományos kérdéscsoportokat vizsgáltak és eltérő vizsgálati módszereket használtak. Ezek az eredmények mind a tájmetriai mutatók ezirányú alkalmazását támasztották alá.

Az első tanulmány egyik fő témája a tájmetriai mutatók szelekciója volt a veresnyakú árpabogár lárváinak kártételének függvényében. Ebben a szelekciós procedúrában a gyakrabban alkalmazott (inter-) korrelációs vizsgálatok mellett (például LI & REYNOLDS 1995; MCGARIGAL & MCCOMB 1995; RIITERS et al. 1995; CUSHMAN et al. 2008), amelyek a szelekciós procedúra első részét képezték, második lépésként egy, a tájanalízisben sokkal ritkábban használt modell-szelekciót AICc-értékek alapján (lásd például SCHINDLER et al. 2015; LUSTIG et al. 2017) alkalmaztam. Ennek az újszerű, kétlépcsős szelekciós procedúrának az eredményei azt mutatták, hogy a legtöbb tájmetriai mutató egymással erősen korrelált, illetve nem nyújtott elegendő magyarázó-erőt a modellekben és emiatt redundáns volt. Egy ilyen szelekciós procedúrának az eredményei természetesen erősen függenek a függő változóktól, illetve azoktól a tudományos kérdésektől, amelyekre válaszokat szeretnénk találni. Ha például azt szerettem volna megvizsgálni, hogy melyek azok a tájmetriai mutatók, amelyek a tájszerkezet időbeli változását a legjobban leképezik, akkor teljesen más eredményeket kaptam volna (lásd például LAUSCH & HERZOG 2002). Ezekből az eredményekből kiindulva azt javaslom, hogy a tájszerkezeti hatások vizsgálatához elég előzetesen egy pár, biológiaiilag

egyszerűen értelmezhető tájmetriai mutatót kiválasztani és ha már ezeknél a mutatóknál szignifikáns hatásokat mérünk, akkor nem érdemes további mutatókat vizsgálni. Mivel a FRAGSTATS a legtöbb tájmetriai mutató kiszámításához a tájfoltok területét vagy kerületét veszi alapul (MCGARIGAL & MARKS 1995; MCGARIGAL et al. 2012), ezért ajánlatos ezzel a két tulajdonsággal szorosan kapcsolódó mutatókkal, mint például a részarányal ('Percentage of Landscape') vagy a szegélysűrűséggel ('Edge Density'), kezdeni. Ennek a módszernek az alkalmazása mind a második, mind a harmadik tanulmánynál sikerrel járt, mivel az összes előzetesen kiválasztott tájmetriai mutató esetében sikerült szignifikáns hatásokat kimutatnom.

Az első két tanulmány esetében egy tájelemzésnél alkalmazott térbeli lépték fontosságának kimutatására az elemzéseknél különböző méretű tájablakokat használtam. A legtöbb vizsgált összefüggés esetében a tájszerkezeti hatások erős lépték-függőséget mutattak. A tájszerkezeti hatások lépték-függőségével ezidáig több, mind növényvédelmi kérdéseket (például THIES et al. 2003; ROSCHEWITZ et al. 2005; THIES et al. 2005), mind rovar-megporzókat érintő kérdéseket (például STEFFAN-DEWENTER et al. 2001; WESTPHAL et al. 2006; SCHERBER et al. 2019) vizsgáló tanulmányban foglalkoztak, de csak ritkán olyan magas, illetve szűk felbontásban, mint az itt bemutatott első két tanulmány esetében. Továbbá ennyi különféle tájmetriai mutatót ezidáig egyetlen ilyesfajta tanulmányban sem vizsgáltak. Az első két tanulmány keretében mért tájszerkezeti hatások lépték-függőségét vizsgálva feltűnő, hogy a legerősebb hatások gyakran 500 méteres léptéken belül fordultak elő. Ilyen kicsi léptékeket általában ilyesfajta vizsgálatoknál sajnos figyelmen kívül szokták hagyni. Ezért azt javaslom, hogy jövőbeli tanulmányok vizsgálatai – legalábbis olyanok, amelyek rovarokkal foglalkoznak – térjenek ki kisebb léptékekre is.

Végezetül össze szeretném foglalni, hogy az értekezés keretében bemutatott három tanulmányban milyen tájszerkezeti hatásokat sikerült kimutatni és hogy ezekből milyen következtetéseket, illetve javaslatokat lehet levonni:

- a) Az első tanulmány eredményei azt mutatták, hogy olyan bűzatóblákban volt erősebb a természetes ellenségek gyérítő hatása, amelyeknek a közvetlen szomszédságában hosszú, de egyben kiterjedt lineáris fás tájlemek (= szélesebb erdősávok) helyezkedtek el. Ezzel szemben nagyobb erdőfoltok (= monokultúras faültetvények) közelében kisebb volt a természetes ellenségek gyérítő hatása. Ezek az eredmények arra engednek következtetni, hogy míg a szélesebb erdősávok valószínűleg élőhelyül szolgálnak a veresnyakú árpabogár természetes ellenségei számára, addig a nagyobb kiterjedésű monokultúras faültetvények számukra nem, vagy legalábbis nem annyira megfelelőek.

- b) A második tanulmány eredményei megmutatták a tájszerkezet kiemelkedő fontosságát egy intenzíven művelt agrártájban a rovarmegporzók, különösen a vadméhek számára. A lágyszárú féltermészetes élőhelyek nagyobb részaránya és/vagy erősebb diszpergáltsága (= térbeli szétdaraboltsága) az összes vizsgált megporzó csoport esetében pozitív hatással bírtak, míg a napraforgótáblák növekvő szegélysűrűsége – vagyis minél több tábla helyezkedett el egy tájablakon belül – a vadméhekre negatív hatással volt. Ezek az eredmények arra utalnak, hogy a napraforgó sikeres megporzásának biztosításához egy intenzíven művelt agrártájban szükség van elegendő nagyságú és kiterjedésű lágyszárú féltermészetes élőhelyre a napraforgótáblák körül. Emellett még az is pozitív hatással lehet a rovarmegporzók viráglátogatási gyakoriságára, ha a napraforgótáblák nem egymás közvetlen szomszédságában helyezkednek el.
- c) Azonban a lágyszárú féltermészetes élőhelyeknek nem csak pozitív hatásai lehetnek. Például a harmadik tanulmány keretében vizsgált alacsony intenzitású mezőgazdasági területek (amelyekbe a lágyszárú féltermészetes élőhelyek is beleszámítottak) nagyobb részaránya és szegélysűrűsége az *Osmia* magányos vadméh-genusz költőkamra számaira negatív hatással voltak. Ezzel szemben például a *Trypoxylon* kaparódarázs pókzsákmányának diverzitására az alacsony intenzitású mezőgazdasági területek részaránya pozitív hatással volt. Ebből arra lehet következtetni, hogy minden tanulmány eredményei nagyban függenek a vizsgált élőlénycsoportoktól és az élőhely típusától, amelyben a vizsgálat folyt. Így szerkezetileg és funkcionálisan hasonló tájelemeknek különféle élőhely-típusokban különböző, akár ellentétes hatásai is lehetnek.

## 5 ÚJ TUDOMÁNYOS EREDMÉNYEK

### Első tanulmány:

- Egy újszerű, kétlépcsős, redundáns tájmetriai mutatók kiválogatására szolgáló szelekciós procedúra kifejlesztése és sikeres tesztelése.
- A veresnyakú árpabogár (*Oulema melanopus*) lárváinak kártétele azokban a búzatáblákban csökkent a legerősebben, ahol a táblák szélétől 200 méteren belül lineáris fás tájelemek (= szélesebb erdősávok) helyezkedtek el. Ezek a lineáris fás tájelemeknek a növekvő szegélysűrűsége és aggregáltsága pozitívan hatottak a kártétel csökkenésére.
- Közeli monokultúrás faültetvények növekvő részaránya mellett viszont a lárvák kártétele kevésbé csökkent. Ez a hatás a táblák szélétől 250 méter távolságra volt a legerősebb.

### Második tanulmány:

- A lágyszárú féltérmezetes élőhelyek, mint például rétek vagy mezsgyék nagyobb részaránya és/vagy erősebb diszpergáltsága a napraforgótáblákat körülvevő tájban növelte a háziméhek, vadméhek és a nem-méh megporzók viráglátogatási gyakoriságát.
- A lágyszárú féltérmezetes élőhelyek pozitív hatásai lépték-függőek voltak, és azok a távolságok, ahol a legerősebb hatások voltak mérhetőek, nagyjából megegyeztek a megfigyelt méh-megporzók átlagos gyűjtési távolságával.
- A felvételezési pontok körül található napraforgótáblák növekvő szegélysűrűsége a vadméhek esetében alacsonyabb viráglátogatási gyakoriságokat eredményezett.

### Harmadik tanulmány:

- Az *Auplopus*, *Megachile* és *Osmia* taxonok fészkeiben található költőkamrák száma szignifikáns összefüggést mutatott a felvételezési helyszínek körül található alacsony intenzitású mezőgazdasági területek részarányával és szegélysűrűségével.
- A *Dipogon* kaparódarázs genusz által zsákmányolt karolópókok (Thomisidae) számára negatívan hatott az alacsony intenzitású mezőgazdasági területek részaránya.
- A *Trypoxylon* kaparódarázs genusz által zsákmányolt pókok Shannon diverzítására viszont pozitívan hatott az alacsony intenzitású mezőgazdasági területek részaránya.

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## 7 AZ ÉRTEKEZÉS TÉMAKÖRÉBEN KÉSZÜLT PUBLIKÁCIÓK

### 7.1 Publikációk lektorált folyóiratokban

LAJOS, K., DEMETER, I., MÁK, R., BALOG, A., SÁROSPATAKI, M. (2021): Preliminary assessment of cavity-nesting Hymenoptera in a low-intensity agricultural landscape in Transylvania. *Ecology and Evolution*, 11(15). doi: 10.1002/ece3.7956

LAJOS, K., SAMU, F., BIHALY, Á. D., FÜLÖP, D., SÁROSPATAKI, M. (2021): Landscape structure affects the sunflower visiting frequency of insect pollinators. *Scientific reports*, 11. doi: 10.1038/s41598-021-87650-9

LAJOS, K., CSÁSZÁR, O., SÁROSPATAKI, M., SAMU, F., TÓTH, F. (2020): Linear woody landscape elements may help to mitigate leaf surface loss caused by the cereal leaf beetle. *Landscape Ecology*, 35, 2225–2238. doi: 10.1007/s10980-020-01097-3

BIHALY, Á., VASKOR, D., LAJOS, K., SÁROSPATAKI, M. (2018): Agrártájba ékelődött természetközeli élőhelyfoltok hatása a napraforgót megporzó rovargyűttekre. *Tájökológiai Lapok / Journal of Landscape Ecology*, 16(1), 45–52.

### 7.2 Konferenciaközlemények és absztraktok

BIHALY, Á. D., LAJOS, K., SAMU, F., FÜLÖP, D., SÁROSPATAKI, M. (2021): A tájszerkezet hatással van a napraforgót megporzó rovarok viráglátogatási gyakoriságára. In: 12. Magyar Ökológus Kongresszus - Előadások és poszterek összefoglalói (p. 144).

LAJOS, K., BIHALY, Á., SÁROSPATAKI, M. (2019): Effects of semi-natural habitats on the abundance and distribution of insect pollinators in sunflower fields in Hungary. In: 10th IALE World Congress - Book of Abstracts (p. 399).

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LAJOS, K., SZALAI, M., TÓTH, F., AMBRUS, G., KISS, J. (2016): A tájszerkezet hatása a veresnyakú árpabogár (*Oulema melanopus*) levélkártételére. *Távérzékelési Technológiák és Térinformatika / Remote Sensing Technologies and GIS Journal*, (6), 476–479.

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Féltermészetes élőhelyek hatása a biológiai kártevő-szabályozásra: a veresnyakú árpabogár  
példája. In: 62. Növényvédelmi Tudományos Napok – *Konferencia kiadvány* (pp. 33–33).

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## **MELLÉKLET**



# Linear woody landscape elements may help to mitigate leaf surface loss caused by the cereal leaf beetle

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## Abstract

**Context** Woody semi-natural habitats serve as permanent habitats and hibernation sites for natural enemies and, through spillover processes, they play an important role in the biological control of insect pests. However, this service is also dependent on the amount and configuration of the dominating woody habitat types: linear landscape elements (hedgerows, shelterbelts), and more evenly extended plantations. Relating natural enemy action to the landscape context can help to identify the effect of woody habitats on biological control effectiveness.

**Objectives** In the Central European agricultural landscapes such as in the Hungarian lowlands, where our study took place, woody linear elements are

characterised by high, while woody areal elements, mostly plantations, by low biological and structural diversity. In this study, we aimed to determine which composition and configuration of woody linear and areal habitats in the landscape may enhance the effect of natural enemy action on plant damage caused by the cereal leaf beetle (CLB, *Oulema melanopus*).

**Methods** Herbivory suppression by natural enemies was assessed from the leaf damage difference between caged and open treatments. These exclusion experiments were carried out in 34 wheat fields on plants with controlled CLB infections. The results were related to landscape structure, quantified by different landscape metrics of both woody linear and areal habitats inside buffers between 150 and 500 m radii, surrounding the wheat fields.

**Results** The exclusion of natural enemies increased the leaf surface loss caused by CLBs in all fields. Shelterbelts and hedgerows in 150–200 m vicinity of the wheat fields had a strong suppressing effect on CLB damage, while the presence of plantations at 250 m and further rather impeded natural enemy action.

**Conclusions** Our results indicate that shelterbelts and hedgerows may provide a strong spillover of natural enemies, thus contribute to an enhanced biological control of CLBs.

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**Keywords** *Oulema melanopus* · Landscape metrics · Natural enemies · Biological control · Exclusion experiments

## Introduction

The importance of semi-natural habitats (SNHs) for natural enemies of crop pests has already been demonstrated in a number of studies (Geiger et al. 2008; Woltz et al. 2012; Alignier et al. 2014; Sarthou et al. 2014). Besides herbaceous SNHs, like grasslands and pastures, woody SNHs are also an important part of the Central-European agricultural landscapes. Such habitat patches roughly fall into two categories. One is elongated, linear landscape elements, such as shelterbelts and hedgerows. These are rather common sights, since they were established as windbreaks along country roads and field boundaries. In Hungary, already in the 1950–1960s their secondary purpose was regarded as providing nesting sites for birds and shelter for natural enemy species, of which many use shelterbelts or hedgerows as foraging habitats, breeding and hibernation sites (Takács and Frank 2009). Commonly, they have a rich understory possessing high biological and structural diversity. Shelterbelts and hedgerows have been shown to enhance the abundance and diversity of natural enemies in the adjacent crop fields, thus supporting the biological control of different agricultural pests (see for instance: Holland and Luff 2000; Kujawa et al. 2006; Thomson and Hoffmann 2009, 2010, 2013; Morandin et al. 2011; Morandin et al. 2014). This has been demonstrated to be based on metapopulation processes which affect the distribution of natural enemies in semi-natural and crop habitat patches at the landscape scale (Samu et al. 2018). An important mechanism that controls this process is the spillover of natural enemies across the non-crop—crop interface, which depends on the habitat identity of the patches, as well as on the structural features of the landscape (Tschardt et al. 2007).

In contrast to linear elements, other woody habitat patches have a more extended area. The naturalness, plant diversity and structural heterogeneity of areal woody areas play an important role in maintaining a diverse natural enemy population and contribute to their spillover (Theron et al. 2020). In Hungary areal

woody landscape elements with higher naturalness are mostly restricted to the highlands of the country (Bartha and Gálhidy 2007). In the lowlands of Hungary, which is the main agricultural area, apart from the few remnant patches of the forest-steppe vegetation (Erdős et al. 2018), the woody areal patches are mostly plantations of poplar (*Populus tremula*), black locust (*Robinia pseudoacacia*) and pines (*Pinus silvestris*, *P. nigra*) with strong canopy closure and predominantly low biological and structural diversity (Weih et al. 2003; Vítková et al. 2017). Moreover, these plantations mostly host forest specialist insects, which are strongly restricted to these habitats and tend to avoid entering more open habitats like cropland, as shown for example for spider and carabid assemblages (Sunderland and Samu 2000; Fischer et al. 2013).

Besides uncovering the habitat preferences of natural enemies, it is also very important to quantify their suppressive impact on agricultural pest activity and damage. This can be experimentally tackled by assessing plant damage when natural enemies can freely act on the pest organism(s) and compare this to situations where natural enemies are excluded by some experimental manipulation. This way, the pest species can cause plant damage unrestricted by their natural enemies (Holland et al. 2012). In cereal fields, however, previous studies have mainly focused their research on the exclusion of the natural enemies of aphids and their relationship with the landscape context, analysing either the relationship between landscape complexity and natural enemy abundance (Caballero-Lopez et al. 2012) or the effects of landscape features, including scale-dependencies, on the outcome of exclusion treatments (Woltz et al. 2012; Martin et al. 2015). The spillover of parasitoid and predatory natural enemies of aphids to crop fields was enhanced by landscape complexity (Thies et al. 2005), but the effect of this process diminished towards field interiors (Zhao et al. 2013).

Apart from aphids, another economically important insect pest of small grain cereals in the northern hemisphere, is the cereal leaf beetle (*Oulema melanopus* L., CLB; Chrysomelidae, Coleoptera). The CLB preferably feeds on cereals like winter wheat, oat, rye and barley (Wilson and Shade 1966). The CLB, originally native to Eurasia, has become lately an invasive pest of small grain crops over large parts of North America (Olfert et al. 2004; Philips et al. 2011).

CLB adults overwinter in ruderal or wooded areas in the proximity of the previous seasons' cereal fields (Casagrande et al. 1977; Philips et al. 2012). They emerge in early spring (Helgesen and Haynes 1972; Gutierrez et al. 1974) and migrate into cereal fields, where females lay 50–300 eggs (Philips et al. 2011) on crop leaves (Helgesen and Haynes 1972). After hatching, the larvae feed on leaves for 10–14 days, during which they pass four instars (Guppy and Harcourt 1978). They skeletonise the leaves by eating the upper epidermis and parenchyma, sparing only the lower epidermis (Gallun et al. 1967), leading to yield losses of up to 40% (Buntin et al. 2004) and a decrease in grain quality (Philips et al. 2011). The biological control of CLBs is well studied, pointing out the important role of both hymenopteran parasitoids (Kher et al. 2011; Philips et al. 2011; Roberts 2016; Kheirodin et al. 2020a), as well as insect and spider predators (Jenser 2003; Kheirodin et al. 2019, 2020a, b). Exclusion trials have already been applied to CLBs, demonstrating that natural enemies increase CLB egg mortality (Meindl et al. 2001).

At our present state of knowledge, however, the landscape context of CLB suppression by natural enemies has seldomly been studied. Tschumi et al. (2015) examined the effect of flowering strips along wheat fields on CLB, on natural enemy abundance and on plant damage in Swiss landscapes with different degrees of complexity. Adjacent flowering strips had a beneficial effect, however this effect was in the given study independent of the landscape context. Another recent study found positive associations of CLB abundance with the land cover of woody SNHs at scales of 1–2 km and negative associations with pastures at 2 km (Kheirodin et al. 2020a, b). However, neither of these studies addressed the effect of landscape configuration on CLB herbivory suppression, nor they examined the effect of woody landscape elements in particular. Woody habitat patches are especially of interest, since the presence of these habitats, contingent on their shape and distribution, benefits the natural enemies, as well as the CLB itself, as they serve as alternative habitats or overwintering sites for both.

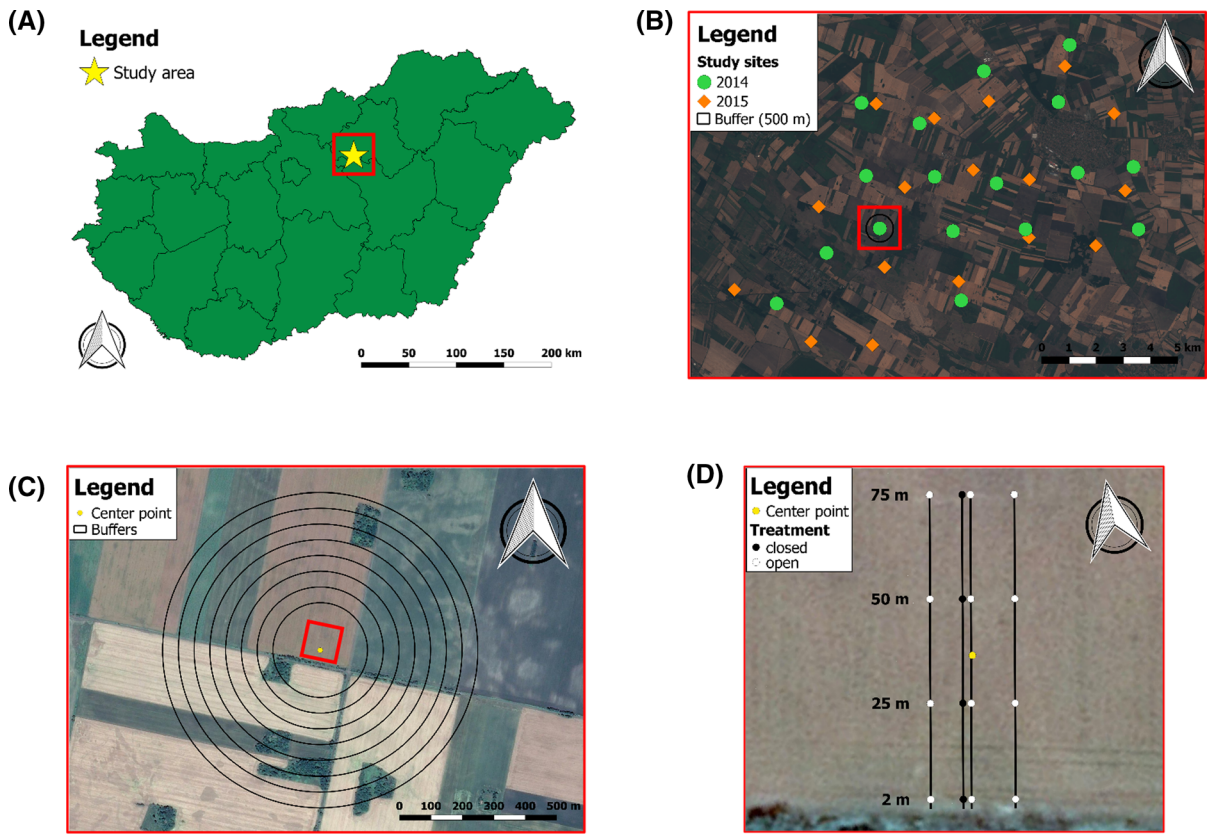
In the present study we aimed to establish the suppression level of natural enemies on CLB damage and its dependence on the extent and configuration of two different types of woody habitats in the landscape, differentiating linear woody elements like shelterbelts

and hedgerows from spatially more extended woody areas like plantations. (1) We hypothesized that natural enemies will reduce CLB herbivory. To test this hypothesis, we have established exclusion trials, predicting that the exclusion of natural enemies should increase the leaf surface loss on wheat plants artificially infested with CLB. (2) Further, we hypothesized that natural enemy action is determined by spillover from neighbouring habitats. This hypothesis was tested by the transect arrangement of the exclusion trials perpendicular to field edge, where we predicted a diminishing suppression effect towards the middle of the field. (3a) Thirdly, we hypothesized that the spatial configuration and distribution of two different types of woody semi-natural habitats in the landscape will have an effect on the suppression of CLB herbivory, expecting that linear woody elements will have a different impact on the herbivory suppression of the CLB compared to spatially more extensive, plantation type woody areas. We also hypothesized that (3b) these landscape effects will be scale-dependent. To test these hypotheses the herbivory suppression effects from the exclusion trials were analysed for potential landscape effects distinguishing between linear and extensive wooded areas in the landscape sectors, considered at multiple spatial scales.

## Materials and methods

### Study area

The study area was located in the north-western part of the Great Hungarian Plain, 80–100 m above sea level, in Jászágó region, Jász-Nagykun-Szolnok County, in an area of approximately 150 km<sup>2</sup> around the settlements of Jászárokszállás, Jászdózsa and Jászágó (Fig. 1a, b). This region has a continental, moderately warm and dry climate with average temperatures between 9.5 and 10.5 °C and average precipitation of 520 mm per year, with a minimum during the summer months. The number of sunshine hours per year is around 2000. Nowadays 90% of the region is under human influence, predominantly agricultural land, and untouched natural areas are rare. The natural and semi-natural habitats in this region are mainly grasslands and pastures with small patches of forest remnants (*Quercus robur*, *Fraxinus excelsior*, *Ulmus* sp.) and with linear riparian forested areas along springs and



**Fig. 1** **a** Location of the study area within Hungary (base map from GADM, the Database of Global Administrative Areas, [www.gadm.org](http://www.gadm.org)). **b** Positions of the 34 investigated wheat fields (the base map is an ESA Sentinel-2 Satellite Image from 2015-07-25). Fields, studied in 2014 are marked green, those in 2015 are orange. **c** Example for the circular buffers between radii of 150 and 500 m drawn around the centre point (yellow),

created to analyse possible scale effects (the base map is a Google Satellite Image from 2014). **d** Schematic drawing of the experimental setup within the landscape sector (the base map is a Google Satellite Image from 2014). The different treatments are indicated with the different colours of the dots. The red frames indicate the position of the consecutive figure (b–d)

small rivers (*Alnus glutinosa*, *Salix* and *Populus* spp. often mixed with introduced species, such as *Acer negundo*, *Celtis occidentalis*, *Ulmus pumila*) (Buschmann 2011; Csiszár 2012). More extended forested areas in the agricultural landscape are dominated by plantations. The most common tree species in plantations in the Jászság region are poplar (*Populus tremula*) and black locust (*Robinia pseudoacacia*) (Buschmann 2011).

#### Experimental setup and management of the focal wheat fields

The field experiments took place in 2014 and 2015. In each year we selected 17 wheat fields as our focal fields (Fig. 1c). The management of all of the fields

was conventional, using synthetic fertilizers. The field sizes ranged from approx. 6 to 100 hectares. The distance between fields studied in the same year was always larger than 1000 m. The majority of the farmers also provided us information about the different wheat cultivars as well as the pesticide used. The most common pre-crop on the investigated fields was oilseed rape (*Brassica napus* L.), followed by sunflower, winter wheat and maize (Online Appendix Table 1). According to our field observations and the database MePAR, all forest patches located inside our landscape sectors were plantations.

In 2014, on each field, we designated three transects (wheat rows, perpendicular to field edge) for the experiments at 10 m distance from each other, plus a fourth one, 2 m left or right of the central row



(Fig. 1d). In each of these four transects we selected individual plants at “transect distances” 2–25–50–75 m from the field edge to serve as host plants for caged populations of CLB adults. Plants were isolated under a mesh (Ikea ‘Teresia’, article number 602.603.30, weight 34 g/m<sup>2</sup>, mesh size 0.25 mm) supported by an iron frame (height 25 cm, diameter 20 cm). The bottom part of the mesh was isolated with washed, clay-free sand to prevent the escape of CLBs as well as the immigration of predators and parasitoids. The cages were set up between 14 and 17 April. Both male and female CLBs were collected with sweep nets, and five individuals, of which at least one was a male, were placed on the isolated individual plants. After 4–7 days the eggs laid were counted and the adults removed. Subsequently, the cages were placed back on plants in the additional central row (= “caged” treatment), while in case of the other rows we did not place back the cages, thus allowing the action of natural enemies (= “open” treatment). We set up a larger number of open wheat plants compared to the caged ones, because we expected higher fluctuations of the CLB herbivory in case of the open ones. The leaf damage caused by the CLB was assessed on 26–27 May. In 2015, in an otherwise identical experimental setup, only three rows were set up per field with the central row receiving the caged treatment and the lateral rows serving as the open treatments. Cage experiments were established on 23–24 April, and the leaf damage was inspected on 17–18 June.

### Response variables

CLB herbivory was quantified as leaf surface loss per experimental wheat plant ( $LSL_{PLANT}$ ), which was visually determined as an average ratio of skeletonized leaf area in relation to the whole leaf area for 10 flag-leaves of the plant. For answering hypotheses (1) and (2) we denoted the response variable as “LSL”, which was calculated as the averaged  $LSL_{PLANT}$  values of the plants at a given transect distance in the given treatment in a field. Thus, in case of the open treatment at each transect distance the LSL value was calculated as the average of  $LSL_{PLANT}$  values of  $N = 03$  or  $N = 02$  plants at the given transect distance observed in the two study years, respectively; whereas in case of the caged treatment for each transect distance LSL was equal to  $LSL_{PLANT}$  of the single plant that was observed.

To answer the landscape context related hypotheses (3a) and (3b) we calculated a single response variable that describes “herbivory suppression” in a given field, which was defined as the difference between the mean leaf surface loss ( $LSL_{DIFF}$ ) of the caged and open treatments. For this we averaged the LSL values across the transect distances separately for the two treatments to receive an  $LSL_{CAGED}$  and an  $LSL_{OPEN}$  value, from which  $LSL_{DIFF}$  values were calculated for all 34 wheat fields according to the following equation:

$$LSL_{DIFF} = \left( 1 - \frac{LSL_{OPEN}}{LSL_{CAGED}} \right) \quad (1)$$

### Mapping of landscape sectors around the fields

The surroundings of the 34 wheat fields were digitised in QGIS 2.18.9 (QGIS Development Team 2009), differentiating between hedgerows, shelterbelts and the woody floodplain vegetation of small creeks (woody linear, WL) and evenly extended forest patches or plantations (woody areal, WA). By our definition, WLs had a minimum width of 1.5 m and a length-width-ratio larger than 3:1. In case of WAs the length-width-ratio did not exceed 3:1. However, ring-shaped woody landscape elements with a length-width-ratio larger than 3:1 as well as irregularly shaped woody landscape elements with narrow parts were also considered as WAs. The minimum mapping unit for woody landscape elements was 100 m<sup>2</sup> with more than 30% shrub or tree canopy cover. The georeferencing of the vector layers was done in the ETRS89/ETRS-LAEA (EPSG: 3035) coordinate reference system. For the digitisation we used Google Satellite Images from 2014 to 2016 as base maps. The identification of the woody landscape elements was always double-checked using the topographic map of Hungary of the open access database MePAR (FÖMI 2016) and satellite images from previous years. The landscape sectors were created in form of circular polygons of 500 m radii around the wheat fields, with the centres of the sampling transects serving as their centre points. These landscape sectors of 500 m radii were used as mask layers to clip layers from a larger digitised map containing the surroundings of the wheat fields. These vector layers were rasterized with an output raster size of 1 × 1 m. The resulting raster

images were sieved for raster cells smaller than 4 m<sup>2</sup> in order to remove lone pixels. Then, smaller, circular landscape sectors starting with radii of 150 m and consecutively increasing by 50 m up to 450 m were drawn around the centre of the 34 transects (Fig. 1c, cf. Thies et al. 2003). These polygons served then as mask layers to clip the basic raster images into images with consecutively smaller extent, resulting in 34 raster images for each of the 8 scales (from 150 to 500 m).

### Calculation and selection of landscape metrics

The raster images of the 34 landscape sectors described above were analysed with FRAGSTATS v4.2.1 in order to determine landscape metrics of the different woody landscape elements. All of the analyses carried out with FRAGSTATS v4.2.1 were performed at the class level with an 8-cell neighbourhood rule. We calculated 36 metrics from the ‘Area and Edge’, ‘Shape’ as well as ‘Aggregation’ metrics categories (McGarigal et al. 2012; McGarigal 2014). In case of 9 from these 36 metrics, besides the ‘regular’ mean value, we also determined the area-weighted mean. Additional statistical data like the median, range, standard deviation or the coefficient of variation of these nine metrics were left out from the calculations. Due to the large number of metrics, however, we decided to conduct a selection procedure on them: (1) We removed those metrics, where too many values were missing (NAs) or zeroes. (2) We also decided to preliminary drop the metrics ‘Total Class Area’, ‘Total Edge’ and ‘Number of Patches’, since they are completely redundant with ‘Percentage of Landscape’, ‘Edge Density’ and ‘Patch Density’. (3) We calculated pair-wise Pearson’s correlation coefficients between the remaining metrics from the largest scale of 500 m for each woody landscape element separately. For the graphical presentation of the results of the correlation analyses we used the R-package ‘corrplot’ (Weih et al. 2003), using the absolute values of the correlation coefficients ( $|r|$ ) and applying a hierarchical clustering (see Online Appendix). Based on the clusters, we aimed to identify different groups of closely related metrics, from which we decided to select one metric to represent each group (Riitters et al. 1995), based on the variance and interpretability of these metrics. These were the metrics “Aggregation Index”, “Edge Density”,

“Largest Patch Index”, “Patch Density” and the mean “Shape Index” for woody linear landscape elements (Online Appendix Table 3) and the metrics “Aggregation Index”, “Related Circumscribing Circle”, “Landscape Shape Index”, “Percentage of Landscape” and the mean value of “Shape Index” for woody areal landscape elements (Online Appendix Table 4). The other metrics were discarded from further analyses. By the above procedure, separately for the linear and areal woody elements, we managed to identify a manageable initial set of quasi-orthogonal, well interpretable metrics that represented the main traits (related to area, edge, shape and aggregation) of these landscape elements, and could serve as a meaningful set of variables from which the effective ones could be selected in a further selection step during model creation (see next section).

### Statistical analyses

To answer the questions in hypotheses (1) and (2) concerning the response variable LSL, we have built Generalised Linear Mixed Models (GLMM) with binomial distribution in R v3.6.3 (R Core Team 2018), using the R-package ‘lme4’ (Bates et al. 2015). In this GLMM, we used the following predictor variables: The ‘treatment’ variable (levels: caged, open), ‘transect distance’ from field edge as a continuous variable, ‘pesticide’ treatment with four levels (‘No Insecticide’, ‘Cyperkill Max’, ‘Decis’ and ‘Karate Zeon’), the area of the studied wheat field as ‘field size’ and the ‘number of eggs’ deposited by the introduced CLB adults at the beginning of procedure as continuous covariates. The ‘field IDs’ and the ‘study year’ were entered as random factors in this model. The binomial GLMM was then tested for over- or underdispersion with the ‘dispersion\_glmmer’ function from the ‘blmecco’ package (Korner-Nievergelt et al. 2015). In case we encountered an over- or underdispersion, we decided to switch to a quasibinomial GLMM using the ‘glmmPQL’ function from the ‘blmecco’ package. When evaluating the final model, in hypothesis (1) we were interested in the treatment effect, while in hypothesis (2) we needed to check the transect distance effect.

Before answering the questions formed in hypotheses (3a) and (3b), we tested the effects of relevant field-level predictor variables (as described above: ‘pesticide’, ‘field size’, mean ‘number of eggs’) on

$LSL_{DIFF}$  and entered ‘study year’ as a random variable in a model. This was done in a linear mixed effect model testing all variables together, since we assumed that the distribution of  $LSL_{DIFF}$  would be closer to a normal distribution. Departure from normality was checked by testing for skewness of  $LSL_{DIFF}$  (package ‘e1071’ by Meyer et al. 2019). Since the values of  $LSL_{DIFF}$  were negatively skewed, we reflected and square-root transformed them in order to fulfil the assumption of normality, which was checked with a Shapiro-Wilk test (Shapiro and Wilk 1965).

To describe how landscape context, stratified by scale levels, affects herbivory suppression ( $LSL_{DIFF}$ ) to answer hypotheses (3a) and (3b), we first studied the spatial autocorrelation structure of this response by calculating Moran’s I values using the R-package ‘ape’ (Paradis and Schliep 2019). The square-root transformed values of  $LSL_{DIFF}$  were then included as dependent variables into linear models with the standardized metrics of woody SNHs as explanatory variables, for each scale separately. We entered the preselected set of explanatory variables into the initial models. To find the most influential variables from this set, we performed automated model selections based on a multimodel inference procedure from the ‘MuMIn’ package (Bartoń 2018). From this multimodel inference procedure, we kept those metrics, which occurred in the models with the lowest AICc values ( $\Delta = 0$ ) and thus have the highest relative importance at multiple scales (Grueber et al. 2011; Symonds and Moussalli 2011). In case this procedure would lead to more than one metric, we would also test the models for multicollinearity between the metrics with Pearson’s correlation analyses, carried out over all spatial scales, and variance inflation factors (VIFs) from the ‘car’ package (Fox and Weisberg 2019). The metrics remaining at the end of this selection procedure were then included in linear models. The fit of all models was a posteriori checked by inspecting residuals and QQ plots.

## Results

### Exclusion effect on CLB herbivory

Testing our first hypothesis, the final binomial GLMM showed that the exclusion of natural enemies had a strong effect on the level of herbivory ( $LSL$ ),

manifesting in highly significantly lower herbivory on the open plants (Table 1). The initial number of eggs ( $68.36 \pm 36.42$  per isolator cage) deposited had a positive, significant effect on herbivory (Table 1). Whereas two of the insecticides applied on the fields—Decis and Karate Zeon—showed weak, but significant effects, decreasing herbivory compared to those wheat fields, where no insecticides were used (Table 1). The variances for the two random effects were 0.5587 in case of the ‘field IDs’ and 0.0001 in case of the ‘study year’. Importantly, in the final model transect distance had no significant effect on herbivory, which contradicted the second hypothesis proposing a diminishing spillover action of the natural enemies further inside the field (Table 1).

### CLB herbivory suppression and woody landscape elements

The linear mixed effect model testing the influence of the independent field-level variables on  $LSL_{DIFF}$  did not indicate any significant effect (Online Appendix Table 2), so none of these variables were included in the final models. The variance of the random effect ‘study year’ was 0. The Moran’s I calculated on the  $LSL_{DIFF}$  data showed no spatial autocorrelation between the sites (observed  $I = -0.038$ ; expected  $I = -0.030$ ;  $p$  value = 0.827), so no correction of the model was necessary.

The results of the landscape analysis gave support to both our hypothesis 3a and 3b. Both types of woody landscape elements showed significant but contrasting effects on CLB herbivory suppression in the studied wheat fields and all these effects were scale-dependent.

In case of WL patches, we found positive, significant effects of the metric ‘Aggregation Index’ on CLB herbivory suppression at multiple spatial scales (Table 2). These effects had their strongest impact at a scale of 200 m. After this peak, there was a rather large drop at 250 m, which was then followed by an increase in the effect strength at 300 m, subsequently reaching a plateau of fluctuating values between scales of 350–500 m. We also found similar positive, significant effects in case of the metric ‘Edge Density’ (Table 2), but at a much narrower range of scales (150–200 m). The effects of ‘Edge Density’ were the strongest at the smallest scale of 150 m, which was followed by a continuous drop of the effect strength to



**Table 1** Results of the binomial GLMM analysing the effects of exclusion treatments and other field scale variables on the LSL (Leaf Surface Loss) of the wheat plants caused by the CLB

Variable	Estimate	Std. error	z value	Pr (> z )
Intercept	1.440	1.158	1.244	0.213
Exclusion treatment (reference level: caged)				
Open	− 4.814	0.724	− 6.650	0.000
Eggs	0.019	0.007	2.925	0.003
Distance from field edge	− 0.004	0.008	− 0.499	0.618
Area of wheat field	− 0.012	0.013	− 0.936	0.349
Insecticide treatment (reference level: No Insecticide)				
Cyperkill Max	1.041	0.916	1.137	0.256
Decis	− 1.717	0.934	− 1.838	0.066
Karate Zeon	− 2.309	0.890	− 2.593	0.010

The variables ‘field IDs’ and ‘study year’ were entered as random factors into the model. For further explanation, see text

**Table 2** Results of the linear model analysing the effects of standardized influential landscape metrics of woody areal SNHs (WA, plantations) on herbivory suppression ( $LSL_{DIFF}$ ), analysed for multiple spatial scales (150–500 m)

Metric	Scale (m)	Estimate	Std. error	t value	Pr (> t )
Percentage of landscape	150	− 0.002	0.001	− 1.544	0.167
	200	− 0.003	0.001	− 3.032	0.013
	250	− 0.003	0.001	− 4.132	0.001
	300	− 0.003	0.001	− 3.064	0.008
	350	− 0.003	0.001	− 2.966	0.007
	400	− 0.003	0.001	− 2.901	0.008
	450	− 0.003	0.001	− 2.889	0.008
	500	− 0.002	0.001	− 2.231	0.035

Influential landscape variables (here only Percentage of Landscape) were selected by automated model selections based on a multimodel inference procedure. For further explanation, see text

a minimum at 300 m. Then, similarly to ‘Aggregation Index’, the effect strength increased again to a plateau of fluctuating values between 350 and 500 m. The effect sizes ( $R^2$ ) of linear models including both metrics were the highest at the smallest scales of 150–200 m, followed by a plateau of low values at 250–300 m and fluctuating values between 350 and 500 m (Fig. 2).

In contrast to WL patches, the metric ‘Percentage of Landscape’ of WA landscape elements had significant, negative effects on CLB herbivory suppression at all scales between 200 and 500 m, with a peak value found at 250 m (Table 3). The effect sizes ( $R^2$ ) of linear models including this metric also had their peak

at 250 m, followed by a rather continuous drop to a minimum at 500 m (Fig. 2).

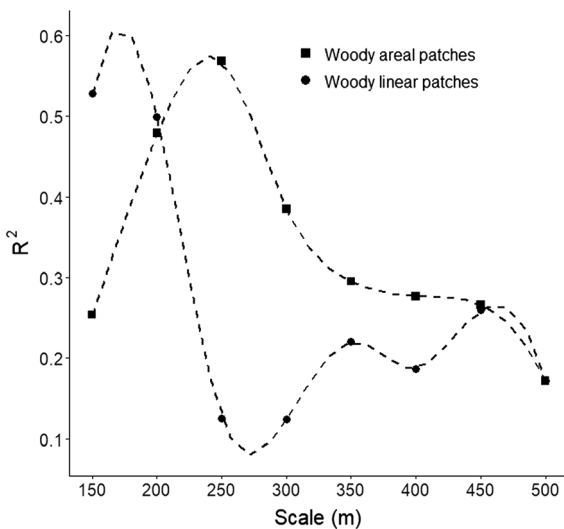
## Discussion

Our results from the exclusion experiments unequivocally supported our hypothesis that natural enemies will reduce the herbivory caused by the CLB. Prohibiting natural enemy access to the artificially infected wheat plants by isolator cages led to a significant increase in CLB herbivory. This coincides with the observation of Meindl et al. (2001), who observed a significantly lower mortality of CLB eggs,

**Table 3** Results of the linear model analysing the effects of influential standardized landscape metrics of woody linear SNHs (WL, shelterbelts and hedgerows) on herbivory suppression ( $LSL_{DIFF}$ ), analysed for multiple spatial scales (150–500 m)

Metric	Scale (m)	Estimate	Std. error	t value	Pr (> t )
Aggregation index	150	0.015	0.005	3.216	0.005
	200	0.009	0.003	3.303	0.004
	250	0.004	0.004	0.993	0.332
	300	0.005	0.003	1.801	0.083
	350	0.011	0.004	2.819	0.008
	400	0.010	0.004	2.438	0.021
	450	0.013	0.004	2.992	0.005
	500	0.011	0.004	2.464	0.019
Edge density	150	0.001	0.000	3.804	0.001
	200	0.001	0.000	2.970	0.008
	250	0.000	0.000	1.336	0.195
	300	0.000	0.000	0.348	0.730
	350	0.000	0.000	1.284	0.209
	400	0.000	0.000	0.818	0.420
	450	0.000	0.000	1.009	0.321
	500	0.000	0.000	0.790	0.436

Influential landscape variables (Aggregation Index and Edge Density) were selected by automated model selections based on a multimodel inference procedure. For further explanation, see text



**Fig. 2**  $R^2$ -values, taken from linear models testing the effects of different landscape metrics of woody linear and areal patches (WL and WA) on CLB herbivory suppression ( $LSL_{DIFF}$ ) for eight spatial scales between 150 and 500 m (see Tables 2 and 3)

when they were protected by isolator cages. However, other than that study we are not aware of any other research that would have assessed natural enemy impact on CLB applying field experimentation. At the same time, for other herbivorous groups there is an overwhelming evidence that natural enemy exclusion will increase herbivory by pests in various crops. In

winter wheat, for instance, flying predators were responsible for 70% reduction in aphid population (Schmidt et al. 2003). In their extensive review Symondson et al. (2002) found that when the action of both generalist and specialist natural enemies were excluded, pest populations were reduced significantly in 89% of cases, and damage was reduced or yield increased significantly in five out of seven cases.

In our experiments, where exclusion was applied in a transect design, the suppressive action of natural enemies was demonstrated at every distance from the field edge, up to the maximal 75 m distance where isolator cages were set up. This result contradicts the observation of some previous studies (e.g. Zhao et al. 2013; Boetzl et al. 2018). However, other studies, like the one conducted by Bowie (1999), got similar results finding no diminishing tendency in the abundance of aphid parasitoids (*Aphidius* spp.) in wheat fields with increasing distance from field edge. Lack of diminishing herbivory suppression towards midfield may either indicate that natural enemy action is not externally influenced or may suggest that spillover from neighbouring habitats has a larger action radius than covered in the present study. We argue, that other results from the present study give support to this latter possibility. In itself, the positive influence of the wooded—non-wooded interface suggests that processes occurring on boundaries, such as a spillover process, play an important role. The peak of this

enhancement for the metric ‘Edge Density’, which is a measure for the amount of boundaries of a landscape element, was between 150 and 200 m and thus larger than the distance we covered with the transect towards the middle of the field. Large spillover radius of natural enemies is important for their efficient plant damage mitigation because *Oulema* spp. densities have been shown to increase towards field interiors in a Belgian study (Van De Vijver et al. 2019). Our estimation of spillover scale is similar to the observations made by Martin et al. (2015), who reported a scale-dependency of landscape effects on the studied parasitoids of aphids, which was the strongest at a scale of 200 m. The results of another study conducted by Evans et al. (2015) also coincide with our observations, who found that the parasitization rate of CLB larvae by *Tetrastichus julis*, a host-specific parasitoid wasp of the CLB, was the strongest at 50–100 m distance from field edge in wheat fields.

The results from the application of insecticides at some of the fields, which occurred as a ‘natural experiment’, may also support our argument about the importance of the spillover process. The application of insecticides had a suppressive effect on the absolute amount of damage caused by the CLB. However, natural enemy action seemed not to be influenced by these chemical treatments, as the differential herbivory between open and caged treatment was not affected by the insecticide application. Indirectly this result allows speculation, that even if short action insecticides also harmed natural enemies, they have been soon replenished, presumably through spillover processes. This dynamism of natural enemies taking refuge in semi-natural habitats during pesticide application and afterwards recolonising crop fields have been demonstrated in a number of studies (Duffield et al. 1996; Gontijo 2019).

We have uncovered that, as we predicted, woody elements in the landscape did influence herbivory suppression in the field. While many studies examined the relationship between landscape complexity and natural enemy abundance and diversity, there are much fewer studies that would directly focus on the relationship between landscape features and pest damage suppression (Chaplin-Kramer et al. 2011; Salek et al. 2018; Kheirodin et al. 2020a, b). Our analysis of woody landscape elements indicated that the extent and type of wooded habitat is important in this regard. Linear wooded habitats, which mostly included shelterbelts

and hedgerows, had markedly increased herbivory suppression. This coincides with other previous observations, like the ones made by Dong et al. (2015), who found that a larger area of shelterbelts resulted in larger ladybeetle abundances through spillover. Linear semi-natural landscape elements, as “green veins” in the agricultural landscape, have been shown to increase the diversity of many organisms, including natural enemies in a wide range of studies (Grashof-Bokdam and van Langevelde 2005). Dabrowska-Prot and Wasilowska (2012) demonstrated that ecotones along habitat boundaries have important function in creating higher diversity, as they comprise specific microhabitats and often have special abiotic characteristics. Shelterbelts significantly increased spider spillover to crop fields in another Polish study (Kajak 2007). The quality and composition of linear woody elements, such as hedgerows, is also an important determinant of natural enemy spillover. High diversity of non-tree woody plants was more valuable for linyphiid spiders, while the presence of trees within hedgerows supported lycosid spiders in an English study (Garratt et al. 2017).

Compared to the positive effects of linear woody elements, however, we found that extensive plantations in the landscape may impede natural enemy action. If the interior of extensive wooded areas has a limited overlap in species composition with agricultural fields, then only limited spillover can be expected. This has been found over a number of case studies in a review by Samu et al. (1999). Predation pressure experiments also indicated a lack of spillover of predators between forested habitats and corn fields (Ferrante et al. 2017). Areal woody elements in the present study were plantations, without exemption. These woody areas in the Hungarian agricultural landscape offer a rather impoverished, homogenised habitat (Bartha and Gálhidy 2007) that is critically different from crop fields. This leaves little space for processes such as landscape complementation or supplementation for potential natural enemy species (Fahrig et al. 2011) and cannot be expected to enhance diversity in the field (Martinez et al. 2015). In this regard areal wooded areas can be considered as a matrix habitat from the perspective of arable natural enemy community, and as such, poor matrix quality will rather have an isolation than an enhancement effect (Prevedello and Vieira 2010; Watling et al. 2011). Furthermore the unfavourable matrix habitat

will impede the dispersion of non-forest species (Vasudev et al. 2015). While not included in our experimental approach, it has to be noted that forested areas may increase CLB density (Kheirodin et al. 2020a, b). Forests offset CLB biological control (Tscharntke et al. 2016) by providing overwintering habitats for adults beetles (Casagrande et al. 1977; Philips et al. 2012) and therefore enhance the spring migration of this pest to cereal fields. However, in other landscape settings, where areal woody areas are more natural and may offer resource supplementation (Erdős et al. 2018; Theron et al. 2020), the trade-off between these areas benefiting both natural enemies and pests might have a different outcome, and may actually tip toward a beneficial role that enhances pest suppression.

The supportive effect of linear wooded elements had a well-defined range of scale, which occurred to be the strongest when these habitats were closer to the focal field and clearly diminished at larger scales (> 200 m). Contrastingly, the inhibiting effect of extensive wooded areas predominantly occurred at larger scales. Scale related effects are often taxon-specific, dependent on dispersal power, life history and several other factors (Thies et al. 2003; Chaplin-Kramer et al. 2011; Martinez et al. 2015) and the observed effects are likely to be the compound action from several natural enemy groups. The typical scale of the suspected spillover process and the type of habitat from which immigration is likely to occur, might give clues, as to which natural enemy groups might be responsible for the observed suppression of CLB herbivory. Hymenopteran parasitoids play a very important role in the biological control of CLBs (Philips et al. 2011; Kher et al. 2014; Roberts 2016) and their spillover can be expected to occur at smaller scales. Especially *Necremnus leucarthros* could be an important natural enemy of the CLB (Jeloková and Gallo 2008) and is one of the most common parasitoid species in Hungary (Szabolcs and Horváth 1991). Laboratory feeding preference trials (Meindl et al. 2001; Kheirodin et al. 2019) and molecular studies on field collected predators (Kheirodin et al. 2020a, b) demonstrated that carabid beetles, lady beetles (Coccinellidae), predatory bugs (Nabidae) and spiders are prominent natural enemies of CLB larvae, adults and also of eggs. Many of these predators have their habitats in forest patches, shelterbelts or hedgerows (Bianchi and Van der Werf 2003). Among the ground-dwelling predators we also have to point out the

potential role of different representatives of ants (Formicidae), which might be responsible for CLB herbivory suppression (Floate and Whitham 1994; Safarzoda et al. 2014).

Finally, we must also point out that in our study the CLB infestation of wheat plants was artificial and that we did not observe any strong infestation of the non-experimental wheat plants in the investigated fields. This phenomenon, along with the basic findings of the exclusion trial, suggests that suppression of CLB damage, as an ecosystem service, works efficiently in the studied landscape. Based on our results we are convinced that we managed to find evidence for the suppressing effects of natural enemy species on the CLB, and could show that woody habitats, pertaining to shape, configuration and scale, importantly enhance this effect. Our study underlines the positive effects of green veining, the preservation and establishment of hedgerows and shelterbelts, which not only helps to enhance biodiversity in the agricultural landscape, but effectively contributes to pest damage suppression in crop fields.

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## Landscape structure affects the sunflower visiting frequency of insect pollinators

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Mass-flowering crop monocultures, like sunflower, cannot harbour a permanent pollinator community. Their pollination is best secured if both managed honey bees and wild pollinators are present in the agricultural landscape. Semi-natural habitats are known to be the main foraging and nesting areas of wild pollinators, thus benefiting their populations, whereas crops flowering simultaneously may competitively dilute pollinator densities. In our study we asked how landscape structure affects major pollinator groups' visiting frequency on 36 focal sunflower fields, hypothesising that herbaceous semi-natural (hSNH) and sunflower patches in the landscape neighbourhood will have a scale-dependent effect. We found that an increasing area and/or dispersion of hSNH areas enhanced the visitation of all pollinator groups. These positive effects were scale-dependent and corresponded well with the foraging ranges of the observed bee pollinators. In contrast, an increasing edge density of neighbouring sunflower fields resulted in considerably lower visiting frequencies of wild bees. Our results clearly indicate that the pollination of sunflower is dependent on the composition and configuration of the agricultural landscape. We conclude that an optimization of the pollination can be achieved if sufficient amount of hSNH areas with good dispersion are provided and mass flowering crops do not over-dominate the agricultural landscape.

### Abbreviations

SNH	Semi-natural habitat
hSNH	Herbaceous SNH
MFC	Mass-flowering crop

The successful cultivation of insect-pollinated mass-flowering crops (MFCs) largely depends on the visiting frequency of different insect pollinator species in the blooming period of these crops<sup>1–3</sup>. It has been shown that the structure of the landscape surrounding fields of MFCs can have a significant impact on pollinator flower-visiting frequency and thus the pollination success of these crops<sup>2,3</sup>. Examples for pollinator-dependent MFCs are oilseed rape (*Brassica napus* L.), sunflower (*Helianthus annuus* L.) or orange (*Citrus × sinensis* L.), which crops are cultivated in monoculture over large areas and bloom synchronously over a short period<sup>3</sup>. In the last few decades, there has been a decline in the abundance and species richness of wild insect pollinators globally<sup>4</sup>. One of the main causes of this process is the homogenisation of agriculturally used landscapes into monocultures with large field sizes at the expense of non-crop areas, resulting in the fragmentation and degradation of semi-natural habitats (SNHs)<sup>4–8</sup>. Examples for woody SNHs are hedgerows, lines of trees, wood- or shrubland areas, whereas herbaceous SNHs comprise habitats such as grass-strips, grassy field margins or grasslands<sup>9</sup>. SNHs in agricultural landscapes can be characterised by significantly lower mechanical and chemical disturbance, and therefore higher stability and plant diversity than crop areas. These areas serve as source habitats for wild pollinators. The decline in source habitat area and subsequent decrease of pollinator densities can lead to significant reductions in the yield of crops that require insect pollination<sup>5,10–13</sup>. Therefore, both for the prevention of further biodiversity loss and for securing pollination of our crops, it is our basic interest to understand the landscape scale dynamics of pollinators and to apply landscape management measures that help to sustain their populations. The influence of landscape structure is especially strong on wild pollinators, which—unlike managed honey bees—permanently live in the area surrounding the MFCs.

Most wild insect pollinator species are sensitive to the amount, composition and configuration of SNHs in the agricultural landscape, because they provide foraging and shelter areas as well as nesting resources for wild

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pollinator groups<sup>2,3,14</sup>. Especially herbaceous semi-natural habitat (hSNH) areas play a crucial role in wild pollinator distribution in the landscape. These areas can support wild pollinator communities throughout the year if the diversity of flowering plants provide nectar and pollen resources over the whole season<sup>15–17</sup>. There have been several studies, which used spatial analysis tools to investigate the effects of the composition and configuration of different landscape elements, primarily SNH patches. For example, habitat area, expressed as the proportion of SNH patches in the landscape, significantly increases the abundance of different solitary pollinator guilds<sup>18,19</sup>. The capacity of such SNH patches to be a source of pollinators is partly area-related, since habitat area sets the carrying capacity for wild pollinators<sup>20</sup>. However, the spillover of wild pollinators from a source patch happens across the edges; therefore edge characteristics are also crucial parameters of spillover<sup>21,22</sup>. If we consider a large patch of a source habitat, then those wild pollinators that stay in the interior of the patch, i.e. their foraging range does not reach the edge of the patch, will not contribute to the spillover process. Similarly, the spatial configuration of source patches is also important, because it affects the mobility and foraging range of different pollinators by determining the probability of a pollinator reaching other habitat patches<sup>23</sup>. Studies carried out in Hungary also showed that a high habitat heterogeneity of the agricultural landscape, such as the presence of herbaceous and woody habitats, and also the inclusion of organic fields among the conventionally managed ones, positively influences the abundance and species richness of wild insect pollinators<sup>24–26</sup>.

Landscape structure can also have a negative impact on the pollinator populations, even apart from the obvious negative effect of the increase in non-flowering crop areas at the expense of SNHs. MFCs, such as oilseed rape and sunflower, offer rich nectar and pollen resource to pollinators, but only temporarily<sup>27</sup>. During blooming period these MFCs redistribute pollinator populations via spillover process from other patches. The distribution of pollinators arises from a dynamic process where different patches attract various proportions of a finite pollinator population<sup>28</sup>. From the perspective of a given patch other patches may play a competing role by depleting the available pollinator population, but in other circumstances may concentrate pollinators from a wider area through resource concentration effect<sup>29</sup>. These processes make the role of MFCs ambiguous in enhancing pollinator populations, and likely dependent on the land-cover and configuration of MFCs and SNH patches in the given landscape.

Besides the composition and configuration of different landscape elements, the possible influence of different spatial scales also has to be taken into account. For example, the results of Tscheulin et al.<sup>30</sup>, who examined the impact of landscape structure on the abundance and species richness of different wild bee species in olive groves, showed that the spatial scales where the strongest correlations occurred corresponded with the size of the investigated wild bee species. The abundance and species richness of wild bees in the olive groves was positively influenced by both area and aggregation related metrics of SNH patches. A meta-analysis of Garibaldi et al.<sup>10</sup> also demonstrated that the visitation rate of all pollinators, except for honey bees, decreased with distance from natural areas. In addition, a marked scale-dependency was found in the mobile group of bumble bees (*Bombus* sp.), where positive effects of SNHs occurred only at > 500 m spatial scales<sup>26</sup>. All these studies indicate that the size and scale-dependent configuration of SNH patches and also of other types of habitats have a strong influence on the abundance and species richness of wild insect pollinators. See Kennedy, et al.<sup>31</sup> for a global quantitative synthesis using a complex configuration metric.

Among MFCs, sunflower (*Helianthus annuus* L.) is grown on more than 4 million hectares in the European Union (= EU-28), making it the second most important oil crop after rape and turnip rape<sup>32</sup>. In Hungary, sunflower is the most important oil crop, cultivated on more than 500,000 hectares since 2005<sup>33</sup>. Even though it is capable of self-pollination, cross-pollination by insect pollinators results in better quality seeds and higher yields<sup>34–36</sup>, up to 40% at field scale<sup>37</sup>. Although, globally viewed, managed honey bee colonies are the main insect pollinators of sunflower (e.g.<sup>38–45</sup>), wild bees, whose role has been less investigated, were found to mostly indirectly, but significantly affect sunflower yield, by increasing the pollination efficiency of honey bees<sup>44,46,47</sup>. Such an effect seems to be aggravated in hybrid sunflower systems where male-sterile (i.e. female only) plants require a polliniser movement for effective pollination<sup>38,39,42,44</sup>. Therefore, in sunflower production in general, it is important to know, which aspects of landscape structure enhance the abundance and species richness of wild insect pollinators. The influence of landscape characteristics on wild pollinators visiting sunflower fields, however, has been rarely investigated<sup>24,48</sup>. It has been shown that a higher amount of SNHs in the landscape surrounding sunflower fields strongly enhances the abundance and species richness of wild insect pollinators<sup>19</sup>. However, the blooming of MFCs can also lead to a depletion of wild pollinator density in the surrounding SNHs, due to their strongly attractive effect on the pollinators<sup>3</sup>, which effect has not been investigated specifically for sunflower fields. For this reason, it is important to fill in the knowledge gap, how the different composition and configuration of the agricultural landscape affect the pollination efficiency of this crop, with special regard that landscape effects might differ between pollinator groups with different foraging ranges and other functional traits.

We focused our study on the most important groups of pollinators of sunflower fields in Hungary: honey bees, wild bees and non-bee insect pollinators. Different pollinator groups interact with landscape structure differently pertaining to their functional traits, such as foraging range, nesting habitats, sociality, and, importantly, if their populations are managed by humans. Functionally, management is an important trait, because bee keepers control managed honey bee population sizes and also their landscape distribution by moving the hives, modifying this way their interaction with the landscape<sup>10</sup>. On the other hand, in wild insect pollinators, which includes both wild bees and non-bee pollinators, populations are governed by natural dynamics being dependent on the amount and distribution of resources provided in the given landscape.

Foraging behaviour covers a range of functional traits, in which respect the most important distinction between the studied groups is whether the species are central place foragers or vagrant, nomadic foragers. Honey bees and all wild bees considered here fall into the central place forager category, because they are all nesting species and all their foraging trips are centred around the nest, irrespective of whether they are social or solitary species. In contrast to bee pollinators, non-bee pollinators encountered in this study were non-nesting. These

pollinators follow a nomadic lifestyle and move on freely from one habitat patch to the next one, meaning that even smaller foraging ranges can add up over time to a larger habitat area covered by their pollination action. In this regard foraging range is a more important trait for central place foragers, because the necessity to return to their nest after a foraging trip will limit their interaction with landscape structure to an area set by this range.

In this study we wanted to know how the structure of our studied landscape, that is the amount and spatial configuration of hSNH patches and sunflower fields occurring in the landscape, affect the sunflower visiting frequency of different pollinator groups. We distinguished three major pollinator groups: managed honey bees, wild bees and non-bees. We also wanted to test the scale-dependency of the landscape effects. For this, we recorded the flower visitation by pollinators in 36 sunflower fields and determined the spatial properties of the two studied landscape elements in increasing sectors around these fields. Our findings indicated that both area and/or dispersion of hSNH patches positively affected sunflower visiting frequency in all pollinator groups. However, for wild bees we also found considerably negative effects of the edge density of sunflower fields. Another interesting finding of our study was that honey bee visitation in sunflower fields was enhanced by an increasing spatial proportion and dispersion of hSNH patches, despite the fact that their hives were artificially maintained and positioned in the landscape.

## Results

**Pollinator assemblage and local effects.** Over the two sampling years we observed 2993 potential pollinators on the investigated sunflower heads (Table S1 A). The vast majority (85.2%) of them were managed honey bees (*Apis mellifera* L.). In comparison, the number of wild pollinators was rather low, with wild bees only making up 7.8% ( $n=233$ ) and non-bee pollinators 7.0% ( $n=209$ ) of the total number of observed pollinators (for detailed numbers see Table S1 A). We were able to identify 103 wild bee specimens at species level. Most of the individuals belonged to the *Lasioglossum* genus (*L. lineare*, *L. malachurum* and *L. politum*), followed by *Bombus* spp. (*B. terrestris*, *B. lapidarius* and *B. pascuorum*), *Andrena flavipes* and *Halictus sexcinctus* (Table S1 B). However, we could not collect and thus were not able to identify the rest of the observed wild bee pollinators ( $n=130$ ) at species level. Among non-bee pollinators (Table S1 B), we found flies (Diptera), mainly hoverflies (Syrphidae: Diptera), and also observed few butterflies (Lepidoptera). But the majority ( $n=166$ ) of non-bee pollinators, predominantly beetles (Coleoptera) and bugs (Heteroptera), was not further classified.

From the field variables only the intensity of cloud cover had a significant, negative effect on the sunflower visiting frequency of wild bees ( $z$ -value =  $-3.131$ ;  $p$ -value =  $0.002$ ; Table S2 A). The distance from field edge significantly affected honey bees as well as wild bees (Table S2 B), which showed a decreasing sunflower visiting frequency with increasing distance from field edge ( $z$ -value =  $-2.468$ ,  $p$ -value =  $0.014$  for honey bees;  $z$ -value =  $-2.918$ ,  $p$ -value =  $0.004$  for wild bees).

**Effects of hSNH patches and sunflower fields on the pollinator groups.** The average proportion of hSNH patches for all 36 studied landscape sectors was nearly constant over all scales, ranging around 9–10%, while the proportion of sunflower fields dropped from nearly 60% at 150 m to ca. 25% at 750 m (Table S3).

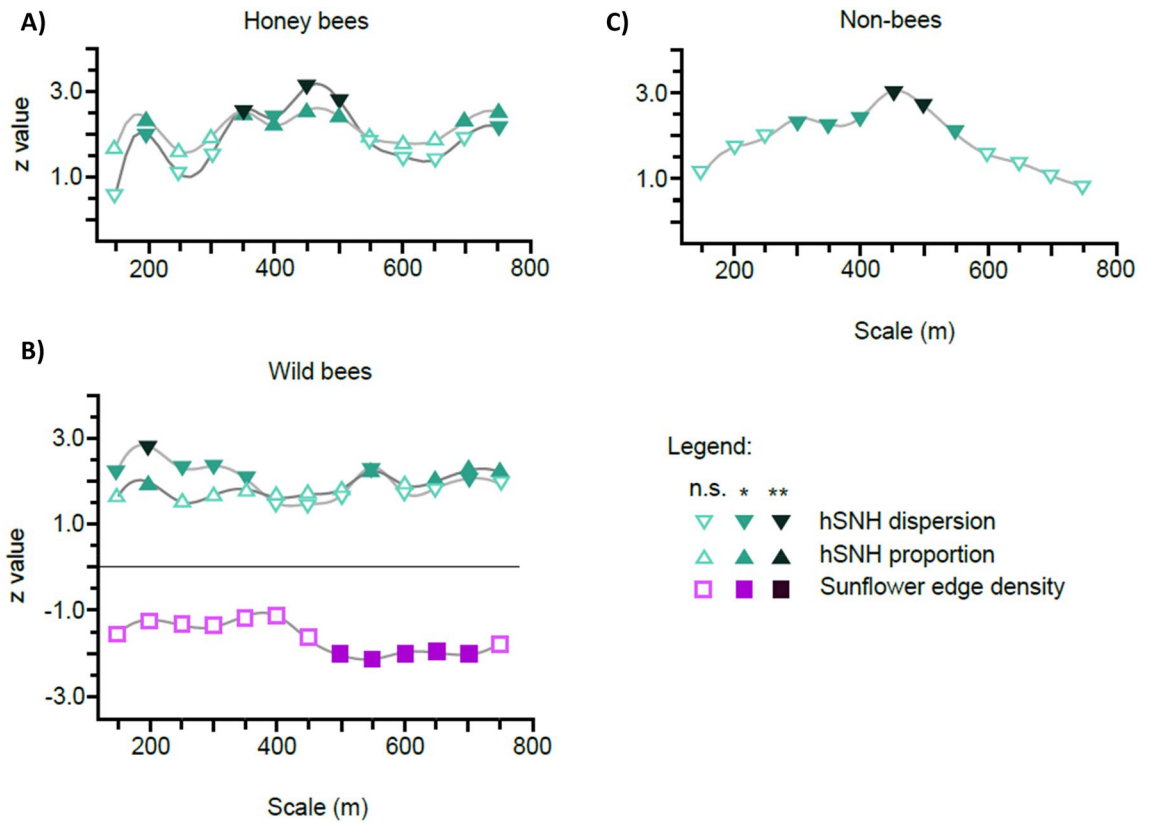
Honey bees, the most abundant sunflower-visiting group, were significantly influenced by the proportion and dispersion of hSNH patches (Fig. 1A; Table S4 A). The spatial properties of sunflower fields in the landscape exerted no significant influence (Table S4 B). The positive effect of hSNH patches was scale-dependent and the strongest at scales between 350 and 500 m.

Considering the two groups of wild pollinators, that is wild bees and non-bee insect pollinators, the Poisson GLMMs revealed that the landscape elements differently affected their sunflower visiting frequency. Similarly to managed honey bees, wild bees were also positively affected by both the proportion and dispersion of hSNH patches. These effects were significant over two distinct ranges of spatial scales, with a gap between 400 and 550 m, where none of the two metrics had significant effects (Fig. 1B; Table S5 A). The impact of the dispersion of hSNH patches was more scale-dependent than of their proportion. While the effects of the dispersion of hSNH patches were significant at smaller scales (150–350 m) and at single larger scales (550 and 700 m), the impact of the proportion of hSNH patches was, except for a significant effect at 200 m, more significant at larger scales (550 and 650–750 m). In contrast to the positive effects of hSNH patches, the edge density of sunflower fields negatively affected the visitation frequency of wild bees, being significant at larger scales (500–700 m). The effects of the proportion and dispersion of sunflower fields was not significant (Table S5 B).

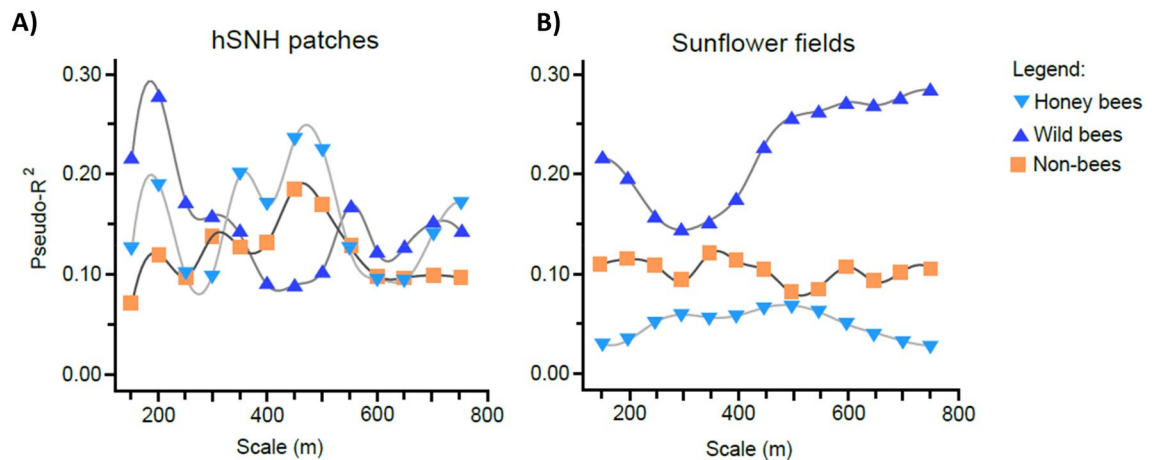
In comparison to the group of wild bees, non-bees were only significantly affected by the dispersion of hSNH patches. This positive effect of the dispersion of hSNH patches was clearly scale-dependent, reaching a peak value at 450 m (Fig. 1C; Table S6 A). Similarly to the group of honey bees, the spatial properties of sunflower fields had no significant impact on non-bees (Table S6 B).

**Comparison of pollinators' scale-dependent responses to hSNH patches and sunflower fields.** We compared the explanatory power of the GLMMs along the investigated scales, separately for hSNH patches and sunflower fields. These show a higher scale-dependency in hSNH influence than in sunflower field influence (Fig. 2A,B). The strongest effect of hSNH patches was found for wild bees, but only at close range (200 m; Pseudo- $R^2=0.281$ ). The effects of hSNH patches on honey bees was more or less trimodal, with moderate effects at close range (200 m; Pseudo- $R^2=0.191$ ) and at the largest scale of 750 m (Pseudo- $R^2=0.174$ ). However, the strongest effects occurred at a medium range of 450 m (Pseudo- $R^2=0.242$ ). Non-bees were also affected the strongest at a medium scale of 450 m (Pseudo- $R^2=0.191$ ).

Sunflower fields had the strongest effects on the group of wild bees, especially at scales over 450 m up to the highest investigated scale of 750 m, with Pseudo- $R^2$  values keeping a high level of 0.233–0.283 in that range. Compared to wild bees, the effects of sunflower fields were considerably weaker for both honey bees (highest



**Figure 1.** Z-values taken from generalized linear mixed models (GLMMs) assuming a Poisson distribution. The Poisson GLMMs tested for the effects of three different landscape metrics of hSNH patches and sunflower fields over 13 spatial scales (150–750 m) on the sunflower visiting frequency of (A) honey bees, (B) wild bees and (C) non-bees. From the three tested metrics only those having significant effects are presented in the figures. For the coefficients of the Poisson GLMMs with all metrics see Tables S4–S6. Trend lines were fitted among the points to make changes in the trend of the z-values more apparent. The intensity of coloration represents statistical significance (n.s. = not significant; \*  $\leq 0.05$ ; \*\*  $\leq 0.01$ ).



**Figure 2.** Explanatory power (= Pseudo- $R^2$ -values) of the Poisson GLMMs from Tables S4–S6, for (A) hSNH patches and (B) sunflower fields over 13 spatial scales (150–750 m). Trend lines were fitted among the points to make changes in the trend of the Pseudo- $R^2$ -values more apparent. The three studied pollinator groups are marked with different colours.

Bee species	Mean foraging distance [reference]	Maximal foraging distance [reference]
<i>Andrena flavipes</i>	150 m <sup>52</sup>	260 m <sup>56</sup> 415 m <sup>52</sup>
<i>Apis mellifera</i>	800 m <sup>57</sup> 1074–1408 m <sup>58</sup> 5500 m <sup>59</sup>	1100 m <sup>60</sup>
<i>Bombus lapidarius</i>	< 500 m <sup>61</sup>	> 300 m <sup>62</sup> 450 m <sup>63</sup> 1500 m <sup>61</sup>
<i>Bombus pascuorum</i>		449 m <sup>63</sup>
<i>Bombus terrestris</i>	270 m <sup>64</sup> 500–1000 m <sup>61</sup>	300–325 m <sup>62</sup> 758 m <sup>63</sup> 800 m <sup>64</sup> 1500 m <sup>65</sup> 1750 m <sup>61</sup>
<i>Lasioglossum malachurum</i>		500 m <sup>53</sup>

**Table 1.** Literature references on mean and maximal foraging distances of some bee species, which were observed and identified in the focal sunflower fields during this study.

Pseudo- $R^2$  value of 0.068 at 500 m) and non-bees (highest Pseudo- $R^2$  value of 0.123 at 350 m). These effects were also clearly less scale-dependent than for wild bees.

## Discussion

The hSNH patches in the studied landscape overall had positive effects on the sunflower visitation of all pollinator groups. The proportion and dispersion of hSNH patches increased sunflower visitation of honey bees and wild bees, whereas visitation frequency of non-bee pollinators was positively affected by the dispersion of hSNH patches alone. Intensive land use in the agricultural region of our study meant that there was a relatively low cover of hSNH patches (c. 10% at each scale) in the landscape sectors around the focal sunflower fields. This low proportion of hSNH patches, which serve as foraging, shelter and nesting areas for many wild bee species<sup>2,3,14</sup>, might also explain the low abundance of wild bees encountered at our study sites. Such a low number of wild bees coupled with a strong dominance of managed honey bees is typical to many agricultural landscapes<sup>25,50,51</sup>. Since we expected a spillover process from semi-natural habitats, the positive effects for the wild pollinator groups were anticipated. However, the positive effect of hSNH patches on honey bees came rather surprisingly, because we hypothesised that positioning of their hives artificially by humans would override landscape effects.

The scale-dependency of the positive effects of hSNH patches (Figs. 1, 2) more or less coincided with the foraging ranges of the observed bee pollinators (Table 1). Studies dealing with the question of foraging range of pollinators found a positive relationship between the body size of pollinators and their foraging distances<sup>52,53</sup>. Table 1 gives an overview of different foraging ranges found in bees in various case studies. Such congruency suggests that the spatial properties of hSNH patches in the landscape may benefit the various pollinator groups in a complementary way, with hSNH patches at different spatial scales having the greatest positive effects on specific groups of pollinators. Although not addressed directly in the present study, among the different bee groups the level of sociality may further influence these pollinators' interaction with the landscape through social information exchange, such as in honey bees, or memorising revisited resource locations, which has been shown for bumble bees and other wild bees<sup>54,55</sup>.

In the case of wild bees we expected the clearest manifestation of landscape effects, because here human management does not directly interfere with their distribution and central place foraging bounds the group more heavily to the given landscape. Mean foraging range of solitary wild bees with small to medium body size have been shown to fall in the 100–300 m range, but maximal distances covered during a foraging trip can be over 1 km<sup>66</sup>. Bumble bees (*Bombus* spp.) were the largest among wild bees in the present study. While bumble bees very effectively utilised resources within 500 m of colonies with a mean foraging distance of workers of only around 270 m<sup>64</sup>, this distance could extend to at least 1.5 km<sup>65</sup>. Sároszpatáki et al<sup>26</sup> found that grassland patches positively affected species richness of bumble bees between 500 and 1000 m and their abundance at 2000 m. The majority of wild bees sampled in our study were small-bodied, projecting short or moderate foraging distances. Indeed, the strongest effects of the hSNH patches found in the present study were at the scales of 150–250 m, with a clear peak value at 200 m. However, an interaction between foraging movement and landscape structure means that pollinator distribution depends not only on foraging traits, but on the landscape characteristics, as well.

Pollinator foraging traits, such as the central place foraging mode of wild bees, might be in interaction with landscape composition and structure. Martin, et al.<sup>23</sup> synthesising studies about 1515 landscapes across Europe, came to the conclusion that spillover of arthropods and arthropod driven services were the strongest when, similarly to our case, SNH landcover was low. Other, patch distribution related landscape characteristics, similarly to our findings, were also important factors for wild bees. In a study, conducted in landscapes in Southern Germany, patch density was positively associated with total wild bee richness<sup>67</sup>. In that study patch density was found to increase the amount of edges and corridors that could act as food and nesting resources and dispersal routes for wild bees. In a wider meta-analysis variation in interpatch distance was shown to be important determinant of social bee abundance<sup>31</sup>, indicating the overall importance of landscape configuration for wild bees.



Honey bees are the most abundant flower visitors worldwide<sup>68</sup>, and were by far the most prominent pollinators of sunflower in our study. With honey bees we can expect that apart from foraging traits and landscape characteristics, human management is also a decisive factor in their pollination efficiency. Honey bees, which can be regarded medium sized among bees, were found to have a mean foraging distance around 800 m, measured from their apiary of origin in a marking study by Hagler, et al.<sup>57</sup>. In the present study the strongest effects of hSNH patches on honey bees were between scales of 350 and 500 m, with a peak at 450 m, which is somewhat lower figure than foraging range reported in the literature (Table 1). However, for honey bees we did not expect any significant effects of hSNH patches, since honey bee workers spread out to flowering fields from artificially and temporarily placed hives. Our initial hypothesis was supported by a synthesis from 29 studies<sup>10</sup>. This review indicated that in contrast to various wild bee groups, whose abundance was influenced differently by isolation from florally diverse natural and semi-natural areas, honey bee visitation did not change with isolation. As opposed to these findings, our results indicated significant positive effects of hSNH patches, related to both their areal extent and level of dispersion in the landscape. We think that the dietary needs of honey bees can offer an explanation for the positive effects of hSNH patches. Nutritional requirements may influence how honey bees forage in landscapes with different floral resources, as collecting pollen from a wide diversity of plants improves their diet composition<sup>69,70</sup>. Several previous studies have already demonstrated that a monofloral diet can have negative impacts on honey bee immune health<sup>71–75</sup>. This improved nutrition secured by a bigger choice of pollen resources can lead to a larger number and also a higher survival rate of the offspring and result in larger hives<sup>71,75</sup>. Compensatory foraging by honey bees can secure essential aminoacid diversity, and likely other nutrients<sup>70</sup>. We suggest that the presence of hSNH patches which offer resources for compensatory feeding will also enhance flower visitation by honey bees in sunflower fields within their foraging range, especially if the florally diverse resources are limited in the landscape. Another possible explanation for this phenomenon could have been that beekeepers preferably put their hives in the vicinity of larger hSNH patches, leading to an accumulation of honeybees in landscape sectors, where the proportion of hSNH patches was large. This pattern, however, could not be verified as there were only two landscape sectors, where beehives were located within the boundaries of the mapped sectors, and the proportion of hSNH patches in these two sectors was actually well below average (c. 3% and 2% of the total landscape sector area at the largest scale of 750 m, respectively).

An interaction between honey bees and wild bees might be important for the success of pollination. Even though honey bees were by far the most abundant pollinators in our study, wild bees may still significantly affect sunflower yield. Pollinator species richness was shown to significantly increase sunflower seed set and production in different studies<sup>46,47</sup>. In a study in hybrid sunflower, where, similarly to our case the large majority of flower visits was by honey bees (72%), behavioural interactions between wild and honey bees increased pollination efficiency of honey bees up to five-fold<sup>44</sup>. In situations, when wild bees were rare, honey bee pollination on average produced three seeds per single visit. However, with higher wild bee abundance honey bee pollination efficiency increased strongly, up to 15 seeds per visit on average. From the study of<sup>44</sup> it became apparent that the presence of wild bees disrupted the flower specialisation of honey bees. After interacting with a wild bee on a male flower 20% of honey bees moved to a female sunflower, whereas only 7% switched after interacting with another honey bee. Also in sunflower, the encounter of honey bees with other bee species, butterflies and moths significantly enhanced honey bee movement among sunflower heads<sup>46</sup>. Furthermore, honey bees after wild bee interaction carried significantly more pollen on their bodies<sup>39</sup>. These behavioural interactions effectively doubled honey bee pollination services on an average hybrid sunflower field<sup>44</sup>.

More sunflower fields in the landscape neighbourhood, expressed by the increasing edge density of the fields, significantly decreased wild bee visitation on the monitored sunflower heads in the focal fields. This effect was the strongest at larger spatial scales (500–700 m). The fact that edge density was the important variable, and not area per se of the surrounding sunflower fields, suggests that sunflowers closer to edges attracted wild bees more than those in the interior of fields. In other words, if sufficient resources were present close to field edges maybe it was not worthwhile to travel greater distances further into the fields for this central place foraging group. This reasoning was supported by the finding that an increasing distance of the monitored sunflower heads from the field edge resulted in significantly lower observed numbers of visiting wild bees, an effect that was also significant for honey bees. Similar observations have already been made in the study of Hevia et al.<sup>34</sup>, who also observed a significant decrease in the numbers of wild bees with increasing distance from the edge of sunflower fields. The visual counts of honey bees were, however, not affected by the distance from field edge in their case.

As opposed to edge density, an increasing areal proportion of MFCs was also reported to have negative effects on pollinators. Across six European regions densities of bumble bees, solitary bees, managed honey bees and hoverflies were negatively affected by the cover of MFCs in the landscape. In SNHs, densities of bumble bees declined with increasing cover of MFCs but densities of honey bees increased<sup>3</sup>. In a German study, at the landscape scale, flowering oilseed rape negatively affected bumble bee densities in SNHs, presumably due to dilution of pollinators, but had a positive effect after flowering, when bees moved back to these SNHs<sup>2</sup>. Despite the temporal increase in floral resources MFCs provide, they overall may limit the growth of pollinator populations, because they fail to provide resource continuity<sup>15</sup> and suitable nest sites<sup>3</sup>. These results together support the ‘landscape-moderated concentration and dilution hypothesis’, which proposes that—such as we found, at least partially, in all pollinator groups—MFCs dilute the density of pollinators, thus weakening pollination services per unit area, but do not affect overall pollinator population size<sup>28</sup>.

**Conclusions.** An increasing proportion and/or dispersion of hSNH patches had positive effects on all studied pollinator groups. All these effects were scale-dependent and corresponded well with the foraging ranges of the observed bee pollinators. Our analysis revealed that pollinator groups reacted to the presence of hSNH patches in a complementary way over the different spatial scales. This meant that these habitat areas had a ben-



**Figure 3.** Example for a landscape sector with a composition of landscape elements typical for the study area. The vector map of the landscape sector was created with the software QGIS 2.18.9 (<http://qgis.osgeo.org>)<sup>76</sup>.

eficial effect at every spatial scale through enhancing one or the other pollinator group, which effect diminished only at distances further than 600 m from the focal fields. As opposed to hSNH patches, sunflower fields in the landscape exerted a negative effect on wild bees. Presumably a higher presence of sunflower diluted wild bee populations, which were bound to a certain area due to their short range central place foraging mode. On all other pollinator groups with larger foraging ranges the effect of sunflower fields was marginal. Our results clearly indicate that the pollination of sunflower is dependent on the composition and configuration of the agricultural landscape. An optimization of the pollination process can be achieved if a sufficient amount of hSNH areas with good dispersion is provided and sunflower fields do not over-dominate. Such landscape configurations promote the beneficial actions of various pollinator groups, which do not only react to landscape structure in a complementary way, but also positively interact with one another to increase pollination efficiency. This case study also points out that studying landscape diversity may uncover ways to landscape optimisation for the benefit of various ecosystem services and the preservation of biodiversity.

## Materials and methods

**Study area and sampling methods.** The study area was located in the central part of Hungary (Jász-Nagykun-Szolnok county), in an intensively used agricultural landscape (Figure S1). The main crops in this region are winter wheat, sunflower and maize<sup>33</sup>. The field experiments were carried out in randomly selected sunflower fields over two years (2014 and 2015), with 18 fields examined in each year with permission of the land owners or farmers (Table S7 A). We made all observations and taking samples from the insect populations with maximal respect to animal welfare. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. Each of the 36 study fields was only sampled once. Field sizes ranged from 1.77 to 108.12 hectares. The fields were located at distances of at least 1.5 km to each other (twice the radius of the landscape sectors, see below). Pollinator data from half of these fields ( $n = 18$  sunflower fields, year 2014) was reported in a Hungarian paper by Bihaly et al.<sup>24</sup>, where no scale-dependent landscape analysis was applied.

The sampling of the pollinators within the sunflower fields happened on July 14–17 in 2014 and on July 10–23 in 2015. On each occasion sampling was performed by visual observation between 9:00 and 17:00, adapted to the daily activity of bees. In each case the percentage of cloud cover and wind velocity was assessed. The sampling was carried out alongside two transects perpendicular to the field edge (Fig. 3), running parallel 10 m from each other. Along a single transect, there were four sampling points located at 5, 25, 50 and 75 m from the edge of the field. At each of these sampling points nine flowering sunflower heads were chosen for observation. These nine sunflower heads were monitored for 10 min by one person, and the pollinator insects, which landed on the flowers and thus may have been involved in the pollination process, were recorded by another person. The same sampling method was also used in Bihaly et al.<sup>24</sup>.

Since we considered the human management of honey bee colonies as a factor that may potentially override landscape effects, we made separate comparison between honey bees and all other non-managed wild pollinators. In the latter group, we introduced a second level of differentiation distinguishing between wild bees and non-bees. Honey bees and bumble bees were identified to species level at the sampling sites. Wild bee species, if we were able to collect them, were sent to a taxonomist for identification. If the sampling of the wild bee species did not happen immediately after their visitation of the sunflower heads, the time was stopped until the pollinator could be caught. The observation period was subsequently prolonged with the time, which was needed for the

sampling. We tried to locate honey bee hives within the mapped landscape sector (up to 750 m). Hives occurred within this area in two sectors. In case of one of these sectors, honey bee hives were placed in the immediate neighbourhood of the sampled sunflower field. Since the number of honey bees sampled in this field was very large ( $n = 354$ ), we excluded honey bee data for this field from further analyses.

**Mapping and calculation of landscape metrics.** In order to reveal possible relationships between the spatial features of different habitat patches and these pollinator communities, the surroundings of the sampled sunflower fields (focal fields) were mapped in QGIS 2.18.9 (<http://qgis.osgeo.org>)<sup>76</sup> using Google Satellite Images from 2014 and 2016 as base maps. The geo-referencing of the vector layers was done in the ETRS89/ETRS-LAEA (EPSG: 3035) coordinate reference system and the minimum area of all digitised patches was 100 m<sup>2</sup>. For testing possible scale-dependent effects, circles of 13 scales with differences of 50 m in radius were created around the centre point of one of the transects (at 37.5 m), ranging from 150 to 750 m (Fig. 3).

We distinguished two landscape element categories, as follows: (1) hSNH patches (herbaceous SNH patches), which were SNH patches with less than 30% shrub or tree canopy cover, like grass strips and pastures; (2) sunflower fields, fields with sunflower as crop in the given season, including the investigated focal fields. The proportion of the two landscape element types and their occurrence per landscape sector are listed in Table S3. The reason behind the separation of the sunflower fields from the other crops and not testing the effects of them was that we assumed that the spatial characteristics of the investigated, focal sunflower field and also that of other nearby sunflower fields may have significant effects on the abundance of the investigated pollinator groups, and they may also interact with one-another (e.g. compete for pollinators). Since none of the major crops besides sunflower was blooming at the time of the field experiments, we did not assume a similar possible influence of other crops. Sunflower fields around the focal fields were identified by ground observations and validated by using satellite images from Google Satellite, Landsat 8 or Sentinel 2A, recorded at multiple different dates between June and October for each sampling year. The correct identification of the hSNH patches was also double-checked using the open access database MePAR<sup>77</sup>.

As a next step, the vector layers of the surroundings were clipped by the circles with the largest radius (750 m). The resulting 36 landscape sectors were then rasterized with an output raster size of  $1 \times 1$  m. The algorithm used was the GDAL command 'Rasterize (vector to raster)', executed as a batch process and with the output resolution set in map units per pixel. The resulting raster images were first sieved for small areas using the GDAL function 'Sieve' with a threshold set at 4 pixels, applying four connectedness (= 4-neighbourhood-rule), and then clipped by the circles with smaller radii, resulting in 36 raster images across 13 scales (from 150 to 750 m).

In order to quantify the spatial composition and configuration of the landscape sectors regarding the two landscape element types, we calculated three specific landscape metrics (also referred to as "metrics") with FRAGSTATS v4.2.1<sup>78</sup>: (1) To quantify the composition of the landscape sectors we chose the metric 'Percentage of Landscape', which measures the proportional abundance of a particular patch type and thus quantifies the areal dominance of that patch type. (2) To quantify the configuration of the two landscape element types within the landscape sectors, we chose the metric 'Edge Density', which gives a measure of the edge length of a particular patch type related to the total landscape area. (3) Finally, we negated the values 'Aggregation Index', which quantifies both the spatial composition and configuration of a landscape unit, to create a metric, which we termed 'Dispersion Index'. The "normal" 'Aggregation Index' quantifies the aggregation of the focal patch type using an adjacency matrix, giving the strength of the aggregation in percent. The value of this index is 0, when the focal patch type is maximally disaggregated and 100, when the patch type is maximally aggregated into a single, compact patch. In our case, the values of the 'Dispersion Index' are turned into the opposite and higher values mean that there is less aggregation or compactness of a particular patch type. So, basically, we created the new metric 'Dispersion Index' mirroring the "normal" 'Aggregation Index'. We also simplified the names of two of these metrics, renaming 'Percentage of Landscape' into 'proportion' and the 'Dispersion Index' into 'dispersion'. The definitions of these three metrics were taken from McGarigal<sup>79</sup>. All calculations were performed at the class level with an 8-cell neighbourhood rule. A good description about these metrics and the concept behind them can be found in the freely accessible lecture notes of Kevin McGarigal<sup>80</sup>.

**Data analysis and presentation.** All analyses were carried out in R 3.6.3<sup>81</sup>. Spatial autocorrelation of the pollinator counts was tested by determining Moran's I values using the R-package 'ape'<sup>82</sup> for each three pollinator groups. The coordinate reference system used for this calculation was ETRS89/ETRS-LAEA (EPSG:3035), which was also used for georeferencing the vector layers. We did not detect any spatial autocorrelation in the field counts of any pollinator group (Table S7 B).

To test the effects of field variables and landscape structure on the sunflower visiting frequency of the three pollinator groups, we applied generalised linear mixed models (GLMMs) assuming a Poisson distribution from the R package 'lme4'<sup>83</sup>, with the site ID as a random factor in each case. The results of the Poisson GLMMs were plotted using the R package 'ggplot2'<sup>84</sup>. All explanatory variables in the GLMMs were continuous ones, except for the study year, which was a categorical variable with the study year of 2014 as reference (Table S2 A). We used the sums of the field counts for the three pollinator groups in all these GLMMs, except for testing the effects of the distance from field edge, where we used the sums of the field counts for each four distances (Table S2 B). For analysing the effects of landscape structure on the sunflower visiting frequency of the studied pollinator groups, we added all three metrics mentioned above as explanatory variables in the Poisson GLMMs, for each two landscape element types separately. This separation was necessary because of the absence of hSNH patches in some landscape sectors at scales below 400 m, while sunflower fields were occurring in all of these sectors (Table S3).

The residuals of all Poisson GLMMs were checked for uniformity, dispersion and outliers using functions from the R package 'DHARMA'<sup>85</sup>. In case the results of these tests would indicate a bad fit of a tested Poisson

GLMM, we intended switch to a negative binomial GLMM. However, this change proved to be unnecessary, since the tests did not detect any significant deviations of the residuals for all tested Poisson GLMMs. All models were also tested for multicollinearity between the explanatory variables with variance inflation factors (VIFs) using the R package ‘car’<sup>86</sup>. The VIFs for the three tested metrics were below 2 at most spatial scales for hSNH patches, but over 2 at the majority of scales for sunflower fields in case of all three pollinator groups, indicating a high redundancy of the metrics for the latter landscape element.

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## Author contributions

K.L. and F.S. took the lead in writing the manuscript; Á.D.B., D.F. and M.S. contributed to writing and provided critical feedback on the manuscript; Á.D.B. and M.S. planned and conducted the field experiments; K.L. created the vector maps and conducted the landscape and statistical analysis; K.L., D.F. and F.S. created the figures.

## Competing interests

The authors declare no competing interests.

## Additional information

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41598-021-87650-9>.

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# Preliminary assessment of cavity-nesting Hymenopterans in a low-intensity agricultural landscape in Transylvania

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## Abstract

In this study, our aim was to assess several traits of cavity-nesting Hymenopteran taxa in a low-intensity agricultural landscape in Transylvania. The study took place between May and August 2018 at eight study sites in the hilly mountainous central part of Romania, where the majority of the landscape is used for extensive farming or forestry. During the processing of the trap nest material, we recorded several traits regarding the nests of different cavity-nesting Hymenopteran taxa and the spider prey found inside the nests of the spider-hunting representatives of these taxa. We also evaluated the relationship between the edge density and proportion of low-intensity agricultural areas surrounding the study sites and some of these traits.

The majority of nests were built by the solitary wasp genus *Trypoxylon*, followed by the solitary wasp taxa *Dipogon* and Eumeninae. Solitary bees were much less common, with *Hylaeus* being the most abundant genus. In the nests of *Trypoxylon*, we mostly found spider prey from the family of Araneidae, followed by specimens from the families of Linyphiidae and Theridiidae. In the nests of *Dipogon*, we predominantly encountered spider prey from the family of Thomisidae. We found significant effects of low-intensity agricultural areas for the genera of *Auplopus*, *Megachile*, *Osmia*, and the Thomisid prey of *Dipogon*. We also found that the spider prey of *Trypoxylon* was significantly more diverse at study sites with higher proportions of low-intensity agricultural areas.

Our results indicate that solitary bees seem to be more abundant in areas, where the influence of human activities is stronger, while solitary wasps seem to rather avoid these areas. Therefore, we suggest that future studies not only should put more effort into sampling in low-intensity agricultural landscapes but also focus more on solitary wasp taxa, when sampling such an area.

## KEYWORDS

landscape context, solitary bees, solitary wasps, spider prey, spider-hunting wasps, trap nests

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## 1 | INTRODUCTION

Several recent studies have reported a decline of insect abundance, biomass, and species richness in many densely populated regions of Western Europe and also other parts of the world (Forister et al., 2019; Habel et al., 2019; Hallmann et al., 2017, 2021; Sánchez-Bayo & Wyckhuys, 2019, 2021). (Wagner et al., 2021) The two main drivers behind this decline are the increasing agricultural expansion and intensification as well as urbanization in these regions, which lead to a loss or fragmentation of the insects' habitats (Habel et al., 2019; Knop, 2016; Merckx & Van Dyck, 2019; Piano et al., 2020; Raven & Wagner, 2021; Sánchez-Bayo & Wyckhuys, 2019, 2021; Wagner, 2020). However, some other recent studies reported a partial recovery of insect abundance, biomass, and species richness in certain Western European regions (like in the Netherlands or Great Britain) since the 1990s, where different kinds of management actions or policies (e.g., stricter regulations of pesticide use, agri-environmental schemes, conservation programs) have been implemented to protect and maintain (insect) biodiversity (Carvalho et al., 2013; Ollerton et al., 2014).

It has already been demonstrated in numerous studies that trap nests are useful tools to assess the biodiversity of cavity-nesting Hymenoptera and also their trophic interactions in a certain area as well as the parasitoids and hyperparasitoids of these Hymenoptera taxa (Albrecht et al., 2007; Klein et al., 2006; Kruess & Tschardt, 2002; Mayr et al., 2020; Scherber et al., 2010; Staab et al., 2018; Stangler et al., 2015; Steckel et al., 2014; Tschardt et al., 1998). Basically, cavity-nesting aculeate Hymenoptera can be divided into two trophic groups of nectar and pollen-feeding solitary bees and predatory solitary wasps (Klein et al., 2006; Mayr et al., 2020; Steckel et al., 2014). With regard to the pollination service provided by cavity-nesting solitary bees, which are pollinators of many wild and crop plant species, and the biological pest control by some cavity-nesting solitary wasp species (like *Ancistrocerus gazella*; Harris, 1994), additional knowledge about these species and the influence of landscape context on them may provide help in measures for their protection.

The fact that trap nests provide a good nesting opportunity and thus lead to an accumulation of cavity-nesting solitary Hymenoptera species living in the area surrounding these nests also makes trap nests especially suitable to study landscape effects. Some studies dealing with the effects of landscape context on cavity-nesting Hymenoptera conducted rather simple landscape analyses looking only at the presence of (Holzschuh et al., 2009; Mayr et al., 2020; Tschardt et al., 1998) or distance from certain habitat types like forests (Klein et al., 2006) or ecological compensation area (ECA) meadows (Albrecht et al., 2007). Other studies, however, looked more specifically at the landscape structure surrounding their study sites, analyzing the effects of the proportion of different habitat types (Coudrain et al., 2016; Kratschmer et al., 2020; Taki et al., 2008) or even conducting complex landscape analyses (Holzschuh et al., 2010; Steckel et al., 2014) at multiple spatial scales (Steckel et al., 2014; Taki et al., 2008).

Most previous studies, which were assessing cavity-nesting Hymenoptera in different Western European countries, were conducted in high-intensity agricultural landscapes (Table 1). However, in the eastern part of Europe, there are still a few regions and areas remaining, which are not under such a strong human influence. An example for such a region is Transylvania in the central part of Romania, where the population density is relatively low and the majority of the landscape is used for extensive farming or forestry. The most common form of extensive farming in this region is traditional small-scale farming, which is characterized by manual hay mowing, manual hay gathering, and extensive low-intensity organic manuring (Babai & Molnár, 2014; Babai et al., 2015). Such small-scale pastures and meadows often harbor a high species diversity of insects and are regarded as high nature value (HNV) grasslands (Veen et al., 2009), which are still widespread in the Transylvanian section of the Carpathian Mountains (Huband et al., 2010). Compared to Western Europe, however, there is a large gap of knowledge concerning the abundance and diversity of cavity-nesting Hymenoptera in Eastern Europe. Up to this date, only a few studies have taken on this topic in Eastern Europe (e.g., Budrys et al., 2010) and no study has addressed this issue in Transylvania. This highlights the need for more studies from such less-disturbed reference landscapes.

Therefore, the goals of our present pilot study were the following: (a) to assess and quantify the abundance and taxon diversity of the cavity-nesting Hymenoptera assemblage in our study area; (b) to identify and quantify the spider taxa preyed by the spider-hunting representatives of the Hymenoptera taxa; (c) to analyze the influence of the proportion and edge density of low-intensity agricultural areas around the study sites on both Hymenoptera and spider prey taxa. Concerning our first goal, we were interested if we would encounter a different taxon composition of cavity-nesting Hymenoptera in the rural, low-intensity agricultural landscape of our study area compared to other, more intensively used Western European study areas (Table 1). Regarding our last goal, we were curious to find out which cavity-nesting Hymenoptera and spider prey taxa would be significantly affected by the proportion and edge density of low-intensity agricultural areas around our study sites.

## 2 | MATERIALS AND METHODS

### 2.1 | Study sites

The study took place in a hilly mountainous area at the border of the two counties Harghita and Kovászna (Transylvania, Romania), where the valleys are predominantly used for extensive, small-scale farming. The landscape surrounding our study sites can be defined as a cultural-historic low-intensity agricultural landscape, which consists of a mosaic of grassland and woodland patches. The grassland patches are mostly used as meadows and pastures, where grazing is made with low numbers of cattle and predominantly hand-mowing is applied (Figure 1). The eight study sites were located in three valleys between 530 and 630 m a.s.l. (Figure S1). The natural vegetation in

**TABLE 1** Examples for studies with a similar study design, analyzing the abundance and diversity of cavity-nesting Hymenoptera, carried out in different Western European countries

Reference	Country	Landscape	Sites	Trap nests	Reeds	Sampling period	Most abundant taxa
Albrecht et al. (2007)	Switzerland	Grassland	13	8	ca. 200	April–October	<i>Trypoxylon figulus</i>
Steffan-Dewenter (2002)	Germany	Agricultural	15	8	150–180	April–October	<i>Osmia bicornis (rufa)</i> ; <i>Hylaeus communis</i>
Diekötter et al. (2014)	Germany	Agricultural	12	2	NA	March–October	<i>Osmia bicornis (rufa)</i>
Fabian et al. (2013) and Fabian et al. (2014)	Switzerland	Agricultural	12	14	170–180	April–October	<i>Osmia bicornis</i> ; <i>Trypoxylon figulus</i> ; <i>Ancistrocerus nigricornis</i>
Gathmann et al. (1994)	Germany	Agricultural	40	6	180	April–October	<i>Megachile</i> sp.; <i>Osmia</i> sp.; <i>Trypoxylon</i> sp.
Happe et al. (2018)	Germany	Agricultural	36	2	NA	April–September	
Holzschuh et al. (2009)	Germany	Agricultural	12	5	ca. 200	April–September	<i>Trypoxylon</i> sp.; <i>Symmorphus</i> sp.
Holzschuh et al. (2010)	Germany	Agricultural	46	2	150–180	April–July	<i>Osmia bicornis (rufa)</i>
Krewenka et al. (2011)	Germany	Grassland	55	216 (total)	ca. 200	April–October	<i>Trypoxylon</i> sp.; <i>Passaloecus</i> sp.
Kruess and Tschardt (2002)	Germany	Grassland	18	4	150–180	April–October	<i>Trypoxylon figulus</i>
Schüppel et al. (2011)	Switzerland	Agricultural	30	2	ca. 170	April–October	<i>Trypoxylon figulus</i> ; <i>Osmia bicornis</i>
Sobek et al. (2009)	Germany	Woodland	12	12	NA	May–September	<i>Ancistrocerus trifasciatus</i> ; <i>Trypoxylon clavicerum</i>

Note: We distinguished three different groups of studies according to the main characteristic of the landscape around the study sites in these studies (=agricultural landscape, grassland, woodland). The number of sites, trap nests per site, reeds (*Phragmites australis* Cav.), the sampling period, and the most abundant taxa reported in these studies are also given. The reed diameters, if reported, ranged from 2 to 10 mm in almost every case.

this region at this sea level mostly consists of sessile oak-hornbeam or hornbeam-sessile oak (*Quercus petraeae*-*Carpinetum* or *Carpino-Quercetum petraeae*) and hornbeam-beech or bastard balm-beech (*Carpino-Fagetum* or *Melittio-Fagetum*) mixed forests (Benke, 2004; Szabó, 1985). Two of these valleys were formed by the Vargyas creek (=‘Vargyas valleys’) and are separated by a canyon (Figure S1A). The third one is located 5–8 km east to the Vargyas valleys and was formed by the Körmös creek (=‘Körmös valley’; Figure S1B). The main flow direction of both creeks in this area is north to south. The Northern Vargyas valley is mostly used for extensive grazing and is dominated by meadows and pastures, while the Southern Vargyas valley, due to its remoteness, is much less used for grazing and more dominated by forest patches. Compared to the two Vargyas valleys, the Körmös valley is more strongly influenced by humans with arable land in its southern part, close to the settlement Erdőfüle (Filia). As a result of these differences in the intensity of land use, the ratio of low-intensity agricultural areas to the natural woodland and other areas in the close surroundings of the eight study sites also differed from site to site (Table S1). We established three sites each in the Körmös valley (K1–K3) and Southern Vargyas valley (SV1–SV3) and two sites in the Northern Vargyas valley (NV1–NV2). The selection of the sites happened randomly, only paying attention to that the center points of each site should be at least 500 m away from each

other. As the majority of the study sites were located within the borders of three Natura 2000 sites (ROSPA0027, ROSCI0036, and ROSCI0091), the number of sampling sites as well as the intensity of the sampling procedure was limited. Natura 2000 sites belong to a large, coordinated network of protected areas in the European Union, which were selected and established with the aim to ensure the long-term survival of threatened species and valuable habitats, listed under both the Birds Directive and the Habitats Directive of the European Commission (European Commission, 2021).

## 2.2 | Trap nests

We installed four trap nests each at the eight study sites at the end of May 2018 (Figure S1). All trap nests were marked with a unique code in reference to the sites and placed within 100 m distance around the center point. The trap nests were custom-made, consisting of a PVC tube of 12 cm diameter and 23 cm length (Figure 2). The tubes were filled with stalks of common reed (*Phragmites australis* Cav.), which were cut off to a length of approx. 22 cm between the nodes, so that the inner part of the stalks would be freely accessible for any nest-building Hymenoptera. The stalks were placed tightly packed in the tubes to avoid them from falling out. The tubes were





FIGURE 1 Typical landscape in the study area



FIGURE 2 A trap nest, mounted to a tree branch

placed in trees or shrubs at 1–2 m above ground. The trap nests were collected at the end of August 2018 and stored outdoors at a shady place. In January 2019, the nests were put into a refrigerator and stored at 4–7°C. In the same month, we began to collect the data from the reed stalks. For this, all stalks were cut open, and, in case we found a nest within a stalk, it was recorded with reference to the unique code of the trap nest plus a serial number, giving each nest a unique ID code. In case of each occupied stalk (=nest), we recorded the following parameters: (a) diameters of the reed stalks; (b) number of occupied brood cells, filled either with Hymenopteran offspring or spider prey (if present)—empty cells were also counted, but not used in further analyses; (c) type of nesting material; (d) color of larvae or cocoons (if present). Besides these parameters, we also counted the total number of stalks per trap nest. Based on the parameters (c) and (d), we were able to identify seven groups of nest types. From each of these seven groups, we also took a few nest samples (at least two) and reared them at room temperature in plastic bags. After the emergence of the adults from these samples, at least two specimens from each nest sample were collected, killed in

70% ethanol, and identified at genus level. We were able to identify the following eight genera: *Ancistrocerus*, *Auplopus*, *Dipogon*, *Hylaeus*, *Megachile*, *Osmia*, *Symmorphus*, and *Trypoxylon*. Except for the two genera *Ancistrocerus* and *Symmorphus* of the subfamily of Eumeninae (potter wasps), which could not be distinguished based on the nest type, each genus was assigned to a specific nest type. Therefore, based on this information, we distinguished between three taxa of solitary bees and four taxa of predatory, solitary wasps, giving them the name of the respective genus, except for the two genera of potter wasps, which were named after the subfamily.

If present, spider prey specimens were collected from the nests, put into 70% ethanol, and marked with the unique nest ID codes. The spider prey were then taxonomically identified at species level—if possible, but at least at family level—and grouped according to the taxon of the spider-hunting wasp and the identified spider families.

### 2.3 | Landscape context

The landscape surrounding the eight study sites was mapped as landscape sectors of 250 m radius in QGIS 2.18.9 (QGIS Development Team 2009) in the ETRS89/ETRS-LAEA (EPSG: 3035) coordinate reference system. We distinguished between three different landscape element types: (a) 'low-intensity agricultural areas' like meadows, pastures, and small patches of arable land (small-scale farming); (b) 'woodland'; and (c) 'other areas', like the water bodies of the two creeks, the creek banks without vegetation, as well as dirt roads. The categories of 'woodland' and 'other areas' were not included in further analyses. We decided to calculate the landscape metrics 'Percentage of Landscape' and 'Edge Density' in FRAGSTATS v4.2.1 (McGarigal et al., 2002) to quantify the landscape structure around the eight study sites (Table S1). We chose these two metrics due to their common use in landscape analysis and their easy interpretability. For calculating the landscape metrics, the vector layers of the landscape sectors were rasterized with an output raster cell size of 1 × 1 m. We used an 8-cell neighborhood rule for all calculations carried out with FRAGSTATS v4.2.1. The calculated values for the proportion and edge density of the low-intensity agricultural areas within 250 m around the eight study sites are listed in the Table S1.

### 2.4 | Statistical analyses

All statistical analyses were conducted in R v3.6.3 (R Core Team, 2020), and all graphs were created using the R package 'ggplot2' (Wickham, 2016). The relationship between the nest numbers of solitary wasp and bee taxa was tested with a generalized linear model (GLM) assuming a Poisson distribution. We conducted principal component analyses (PCAs) using functions from the R packages 'FactoMineR' (Le et al., 2008) and 'factoextra' (Kassambara & Mundt, 2020). These PCAs were used to reveal if there was a relationship between the study sites and the nest

numbers of the Hymenopteran taxa and the specimen numbers of the most commonly preyed spider families, that is the families of Araneidae, Linyphiidae, and Theridiidae for *Trypoxylon* (all above 100 specimens) as well as Thomisidae, which was the most frequently preyed spider family for *Dipogon*. All variables were scaled prior to the PCAs. The differences in the reed stalks' diameter used by the Hymenopteran taxa for nesting were tested with an ANOVA followed by a post hoc Tukey's HSD test (confidence level = 0.95). The relationship between the number of nests and occupied brood cells for the seven cavity-nesting Hymenopteran taxa was tested with linear models (LMs).

We applied generalized linear mixed models (GLMMs) assuming a Poisson distribution from the R package 'lme4' (Bates et al., 2015) to analyze the effects of the proportion and edge density of the low-intensity agricultural areas on the cavity-nesting Hymenopteran taxa and the most commonly preyed spider families. In these GLMMs, we used the number of occupied brood cells (=parameter  $b$ ) per site for all seven cavity-nesting Hymenopteran taxa and the number of preyed spider specimens per site for the most frequently preyed spider families. The number of occupied brood cells was chosen, because it showed a considerably higher variance than the number of nests for rarer taxa. The IDs of the eight study sites were included as a random effect in all GLMMs. The metrics of low-intensity agricultural areas were scaled prior to the GLMMs.

The relationship between the proportion and edge density of the low-intensity agricultural areas and the diversities per site for both Hymenopteran taxa and *Trypoxylon* spider prey was analyzed with linear models (LMs). The diversity of both groups was assessed by calculating Shannon's Diversity Indices (SDIs) using the R package 'vegan' version 2.5-6. (Oksanen et al., 2019). The SDIs were determined using the number of occupied brood cells per site for the Hymenopteran taxa and the number of spider specimens per site for the spider families preyed by *Trypoxylon*. For the *Trypoxylon* spider prey diversity, the specimen numbers from all seven identified spider families were used for determining the SDI. The distribution of both SDIs fulfilled the assumption of normality. The metrics of low-intensity agricultural areas were scaled prior to the LMs.

The residuals of all LMs, GLMs, and GLMMs were tested for uniformity, dispersion, and outliers using functions from the R package 'DHARMA' (Hartig, 2020). We did not detect any significant deviations for the residuals of the tested models. Finally, we also checked for spatial autocorrelation (Moran's  $I$ ) in the case of those data, where we encountered a significant effect of the landscape context, using the R package 'ape' (Paradis & Schliep, 2019). The coordinate reference system used for this analysis was ETRS89/ETRS-LAEA (EPSG: 3,035), the same one as used for mapping. We only detected significant spatial autocorrelation in the case of the brood cells of the genus *Megachile* (Table S2). Therefore, besides the normal linear regression models, we also used generalized least squares fits ('gls') by REML from the R package 'nlme' (Pinheiro et al., 2013), incorporating a Gaussian correlation structure in order to account for the spatial autocorrelation in case of *Megachile*. The brood cell numbers of *Megachile* were "log+1"-transformed for this analysis.

### 3 | RESULTS

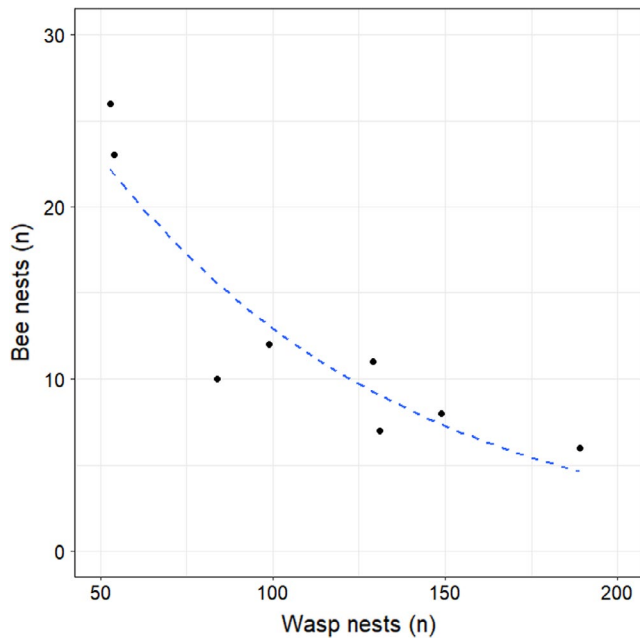
#### 3.1 | Nests

In total, we found 990 nests in 4,857 reed stalks, with the occupancy per site ranging from ca. 13%–30% with a mean number of  $20 \pm 6\%$  for all sites (Table S3A). The majority of the nests were built by solitary wasps ( $n = 888$ ; Table S3B), with the genus *Trypoxylon* ( $n = 560$ ) being the most abundant nest-building taxon at five of the eight study sites, especially at those located in the Southern Vargyas valley (SV1–SV3). We found 158 nests built by the wasp genus *Dipogon*, which was the most abundant nest-building taxon at two study sites (K3 and NV1). The nests of *Dipogon* occurred at all sites, but always in a balanced manner with nest numbers ranging between 8 and 27 ( $19.75 \pm 6.76$  nests per site on average). We identified 152 nests built by representatives of the subfamily of potter wasps (Eumeninae). The nests of potter wasps were found at all sites, but with strongly varying numbers, ranging from the most abundant nest-building taxon at one site (K1 with 51 nests) to nearly absent at another site (K3 with 2 nests). Nests of the wasp genus *Auplopus* occurred at seven of the eight study sites, but always with very low numbers ( $n = 18$  in total).

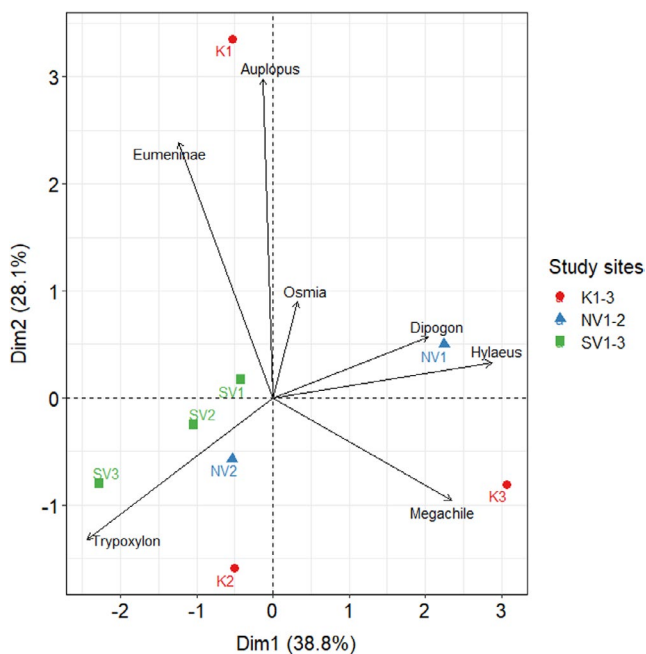
The number of nests built by solitary bees was relatively low compared to those built by solitary wasps ( $n = 102$ ; Table S3B). We found a total of 61 nests built by the genus *Hylaeus*, followed by the genera *Osmia* ( $n = 23$ ) and *Megachile* ( $n = 18$ ). From these solitary bee genera, only nests built by *Hylaeus* were occurring at all sites. We also observed that an increasing number of wasp nests encountered at a study site had a significantly negative effect (Estimate =  $-0.01$ ;  $df = 6$ ;  $z$  value =  $-4.61$ ;  $p$ -value  $< 0.001$ ) on the number of bee nests (Figure 3).

The PCA (Figure 4) conducted on the nest data also indicated that the nest numbers of *Trypoxylon* were most strongly associated with the study site SV3 and less strongly with four other study sites (K2, NV2, SV1, and SV2). The nest numbers of the other cavity-nesting Hymenopteran taxa were most strongly associated each with one site (*Dipogon*, *Hylaeus* with NV1; *Auplopus* and Eumeninae with K1; *Megachile* with K3). Only the nests of *Osmia* had no clear association with any site.

We partially found differences in the diameters of the reed stalks, which the Hymenopteran taxa used for nesting (Figure 6). Overall, the occupied reed stalks (=nests) had a mean diameter of  $6.62 \pm 0.33$  mm (Table S3A). The genus of the small-sized solitary bee *Hylaeus* built its nests in stalks with the smallest diameters ( $5.68 \pm 0.75$  mm). The three most common wasp taxa found in the trap nests—*Trypoxylon*, *Dipogon*, and Eumeninae—all choose reed stalks of very similar diameters, which were close to the overall mean diameter of all reeds with nests inside ( $6.57 \pm 1.02$  mm for *Trypoxylon*;  $6.45 \pm 0.82$  mm for *Dipogon*;  $6.62 \pm 1.19$  mm for Eumeninae). The two medium-sized solitary bee genera *Osmia* and *Megachile*, as well as the Pompilid wasp *Auplopus*, which builds nests with barrel-shaped cells, all favored reed stalks with larger diameters: *Osmia* ( $7.45 \pm 1.40$  mm), *Megachile* ( $8.44 \pm 1.19$  mm), and *Auplopus* ( $8.21 \pm 0.89$  mm).



**FIGURE 3** Relationship between the number of wasp and bee nests at the eight study sites. The dashed blue line represents a generalized linear model (GLM) assuming a Poisson distribution, fitted to the data points



**FIGURE 4** Principal component analysis (PCA) biplot of the nest numbers of the cavity-nesting Hymenopteran taxa per site. The length of the arrows represents the strength of the association with the study sites

Regarding the number of occupied brood cells per site (Table S3C), we found significant relationships between the number of nests and cells for all Hymenopteran taxa (Table S4A). The genus *Dipogon* had the lowest mean number of cells per nest (<3), while *Auplopus* and *Osmia* had the highest numbers of cells per nest (>4) from all Hymenopteran taxa (Table S4B).

### 3.2 | Spider prey

The largest number of identifiable spiders was preyed by *Trypoxylon* with a total number of 1,471 specimens (Table S5A), followed by *Dipogon* with 99 identifiable specimens (Table S5B) and *Auplopus* with only one identifiable specimen from the family of Clubionidae at the NV1 site. The majority of spiders preyed by *Trypoxylon* were from the family of Araneidae ( $n = 1,118$ ). Among Araneidae, *Mangora acalypha* was the most abundant species, occurring in 14 different nests ( $n = 17$ ). Other spider families, which were more commonly preyed by *Trypoxylon*, were the Linyphiidae ( $n = 175$ ), with *Linyphia triangularis* as the most abundant species encountered in 18 different nests ( $n = 44$ ), and the Theridiidae ( $n = 131$ ), with *Phylloneta impressa* as the most common species found in 14 different nests ( $n = 53$ ). Other spider families preyed by *Trypoxylon* were the Tetragnathidae ( $n = 31$ ), Thomisidae ( $n = 10$ ), Salticidae ( $n = 4$ ), and Trachelidae ( $n = 1$ ). *Dipogon* clearly differed in its prey use from *Trypoxylon*, with mostly preying on spiders from the family of Thomisidae ( $n = 93$ ). The most abundant species from this family found in *Dipogon* nests were *Xysticus bifasciatus* ( $n = 4$ ) and *Xysticus cristatus* ( $n = 4$ ). The PCA (Figure 6) conducted on the numbers of the four most common spider prey families of *Trypoxylon* and *Dipogon* showed that the Araneid prey of *Trypoxylon* and Thomisid prey of *Dipogon* were mostly related to the study sites in the Southern Vargyas valley (SV1-SV3), whereas the Linyphiid and Theridiid prey of *Trypoxylon* were strongly associated with the K2 site.

### 3.3 | Low-intensity agricultural areas

The cell numbers of the Hymenopteran taxa of *Auplopus*, *Megachile*, and *Osmia* were significantly correlated with both the edge density and proportion of low-intensity agricultural areas around the study sites (Table 2). The strongest, significant relationships with low-intensity agricultural areas were found for *Osmia*, where an increasing edge density and proportion of these areas both had negative effects on the cell numbers of this bee genus (Table 2). The cell numbers of the *Auplopus* wasp genus were significantly, positively correlated with an increasing edge density and negatively with an increasing proportion of low-intensity agricultural areas (Table 2). The cell numbers of the *Megachile* bee genus were significantly, positively correlated with both an increasing edge density as well as an increasing proportion of low-intensity agricultural areas (Table 2). However, the effects of both the edge density (Estimate = 0.01;  $t$ -value = 1.80;  $p$ -value = 0.12) and proportion of low-intensity agricultural areas (Estimate = 0.02;  $t$ -value = 0.60;  $p$ -value = 0.57) were not significant in the models corrected for spatial autocorrelation.

The number of *Trypoxylon* and *Dipogon* spider prey was largely unaffected by the edge density and proportion of low-intensity agricultural areas around the study sites (Table 3). From the preyed spider families, only the numbers of Thomisidae were significantly, negatively correlated with an increasing proportion of low-intensity agricultural areas (Table 3).



The edge density and proportion of low-intensity agricultural areas had no significant effects on the SDI of the nest-building solitary Hymenopteran taxa at the study sites (Table 4). The SDI of the *Trypoxylon* spider prey, however, was significantly, positively influenced by the proportion of low-intensity agricultural areas around the study sites (Table 4).

## 4 | DISCUSSION

### 4.1 | Nests

Analyzing the content of the trap nests revealed that the nest numbers of solitary wasps were higher than the nest numbers of solitary bees across all study sites. Nests built by solitary bees were only more frequently found at two sites (K3 and NV1), where the numbers of wasp nests were relatively low. From these two sites, NV1 was located the closest to the border of the Natura 2000 site 'ROSPA0027' framing the two Vargyas valleys and K3 was completely situated outside the Natura 2000 site 'ROSCI0091', which extends over the eastern part of the Körmös valley (Figure S1A and B). Thus, an increasing nest number of solitary bees might be the indication of an increasing human impact at the study sites.

**TABLE 2** Results of generalized linear mixed models (GLMMs) assuming a Poisson distribution, testing for the relationship between the proportion and edge density of low-intensity agricultural areas within 250 m around the eight study sites and the total number of occupied brood cells per nest and site, built by different cavity-nesting Hymenopteran taxa

Metric	Taxon	Estimate	SE	z value	Pr(> z )
Edge density	Bees	0.00	0.00	0.00	1.00
	Wasps	0.00	0.00	-1.33	0.18
	<i>Auplopus</i>	0.01	0.00	<b>1.99</b>	<b>0.05</b>
	<i>Dipogon</i>	0.00	0.00	-0.29	0.77
	Eumeninae	0.00	0.01	-0.15	0.88
	<i>Hylaeus</i>	0.01	0.01	1.31	0.19
	<i>Megachile</i>	0.02	0.01	<b>2.06</b>	<b>0.04</b>
	<i>Osmia</i>	-0.01	0.00	<b>-2.15</b>	<b>0.03</b>
	<i>Trypoxylon</i>	-0.01	0.01	-1.57	0.12
Proportion	Bees	0.00	0.01	0.03	0.97
	Wasps	-0.02	0.01	-1.89	0.06
	<i>Auplopus</i>	-0.02	0.01	<b>-3.05</b>	<b>0.00</b>
	<i>Dipogon</i>	-0.02	0.01	-1.28	0.20
	Eumeninae	-0.03	0.03	-0.98	0.33
	<i>Hylaeus</i>	0.02	0.02	0.64	0.52
	<i>Megachile</i>	0.08	0.04	<b>2.18</b>	<b>0.03</b>
	<i>Osmia</i>	-0.03	0.00	<b>-6.61</b>	<b>0.00</b>
	<i>Trypoxylon</i>	-0.03	0.02	-1.30	0.20

Note: The IDs of the sites were included as a random effect in these GLMMs. The number of observations was 8 in each case. Significant relationships are marked bold.

Solitary bees were also the most abundant taxa in the majority of those Western European studies that were conducted in high-intensity agricultural landscapes (Table 1), whereas in studies, that were carried out in natural (Sobek et al., 2009) or low-intensity agricultural (Albrecht et al., 2007; Krewenka et al., 2011; Kruess & Tschardtke, 2002) landscapes with higher proportions of grass- or woodland, solitary wasp taxa were the most abundant nesting taxa. The results of the PCAs also indicated that the occurrence of the most abundant cavity-nesting Hymenopteran taxon *Trypoxylon* showed the strongest association with study sites located in the Southern Vargyas valley, where human disturbance is relatively low. Another possible explanation for low numbers of bee nests is that competitive pressure from higher wasp densities caused solitary bee taxa to search for alternative nesting locations. This theory is partially supported by the reed diameters chosen for the nests of the most common solitary wasp taxa (= *Trypoxylon*, *Dipogon*, and Eumeninae; Figure 5), which were very close to the overall mean diameter of all reeds with nests inside (=  $6.62 \pm 0.33$  mm). This indicates that reed stalks with average diameters were preferably occupied by the most abundant Hymenopteran taxa, leaving the other, rarer taxa only stalks with much smaller or larger diameters for nesting (Figure 5). Using a specific reed diameter for nesting, however, could also be related to the body size or proportions of the Hymenopteran taxa. For example, the smallest taxon *Hylaeus* also choose reeds with the smallest diameters for its nests (Figure 5). It is also possible that the sampling period of our study did not overlap well with the breeding time of the local solitary bee taxa. The results of another study using sweep-net methods, conducted parallel to this one during 2018 in the same area, support this theory as they revealed that the occurrence of *Osmia* species was mainly in spring (April and May), while their occurrence between June and August, the time when the trap nests were available for them, was considerably lower (Demeter et al., 2021).

### 4.2 | Spider prey

We found that the majority of spider specimens preyed by the genus *Trypoxylon* were from the family of Araneidae. In contrast to our findings, however, two other studies reported that the majority of spider specimens preyed by *Trypoxylon figulus* were from the family of Theridiidae (Coudrain et al., 2013; Hoffmann et al., 2020). A possible explanation for the different findings of these two studies is that they were carried out in more intensively used agricultural landscapes. The results of the PCAs also support this assumption as they indicate that the Araneid prey of *Trypoxylon* was closely related to the study sites located in the remote Southern Vargyas valley (SV1-SV3), where the proportions of low-intensity agricultural areas were considerably lower than at the other study sites. However, the Theridiid prey of *Trypoxylon* was strongly associated with the study site K2, where low-intensity agricultural areas were the proportionally most dominant landscape element (Figure 6).

Metric	Family	Estimate	SE	z value	Pr(> z )
Edge density	Araneidae (Try)	-0.02	0.01	-1.84	0.07
	Linyphiidae (Try)	0.00	0.01	-0.23	0.82
	Theridiidae (Try)	-0.01	0.01	-1.08	0.28
	Thomisidae (Dip)	0.00	0.01	-0.57	0.57
Proportion	Araneidae (Try)	-0.07	0.04	-1.70	0.09
	Linyphiidae (Try)	0.01	0.04	0.40	0.69
	Theridiidae (Try)	0.01	0.05	0.19	0.85
	Thomisidae (Dip)	-0.06	0.01	<b>-9.41</b>	<b>0.00</b>

Note: The IDs of the sites were included as a random effect in these GLMMs. The number of observations was 8 in each case. Significant relationships are marked bold.

Diversity	Metric	Estimate	SE	t-value	Pr(> t )
Hymenopteran	Edge density	0.00	0.00	1.17	0.29
	Proportion	0.00	0.00	1.37	0.22
Spider prey	Edge density	0.01	0.01	0.62	0.56
	Proportion	0.03	0.01	<b>4.38</b>	<b>0.00</b>

Note: For the calculation of the SDIs for the *Trypoxylon* spider prey, representatives of all spider families preyed by *Trypoxylon* (Table S5A) were included. The number of observations was 8 in each case. Significant relationships are marked bold.

### 4.3 | Low-intensity agricultural areas

The brood cell numbers of *Osmia* were significantly lower at study sites with both a higher edge density and proportion of low-intensity agricultural areas. This finding may come a bit unexpected, since most *Osmia* species feed on wild flowers, but many species are closely associated with forest habitats due to their nesting habits as they create small burrows for their nests in tree barks (Müller et al., 2019). In contrast to *Osmia*, a higher edge density and proportion of low-intensity agricultural areas both had a significantly positive effect on the brood cell numbers of *Megachile*. The brood cell numbers of the Pompilid were *Auplopus* were positively correlated with an increasing edge density, but negatively with an increasing proportion of low-intensity agricultural areas. This latter finding corresponds well with those reported by Holzschuh et al. (2009), who found that the abundance of Eumenid, Pompilid, and Sphecid wasps were highest at forest edges, which provide natural nesting sites, and lowest in grass strips, with a few natural nesting sites. They also reported that wasp abundance in grass strips connected to forest edges was higher than in slightly isolated grass strips and much higher than in highly isolated grass strips.

We did not detect any significant relationship between the edge density or proportion of low-intensity agricultural areas and the diversity of the nest-building solitary Hymenopteran taxa. Other studies, however, found that landscape context had significant effects on Hymenopteran species diversity: Steffan-Dewenter (2002) reported a positive relationship between an increasing proportion of semi-natural habitats and the number of Hymenopteran species, while Schüepp et al. (2011) found that species richness of wasps was more than doubled and diversity three-times higher at sites with high

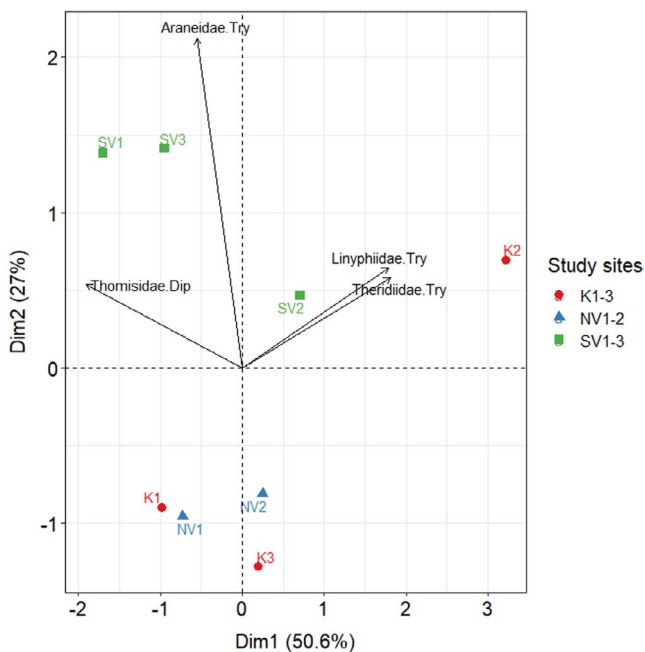
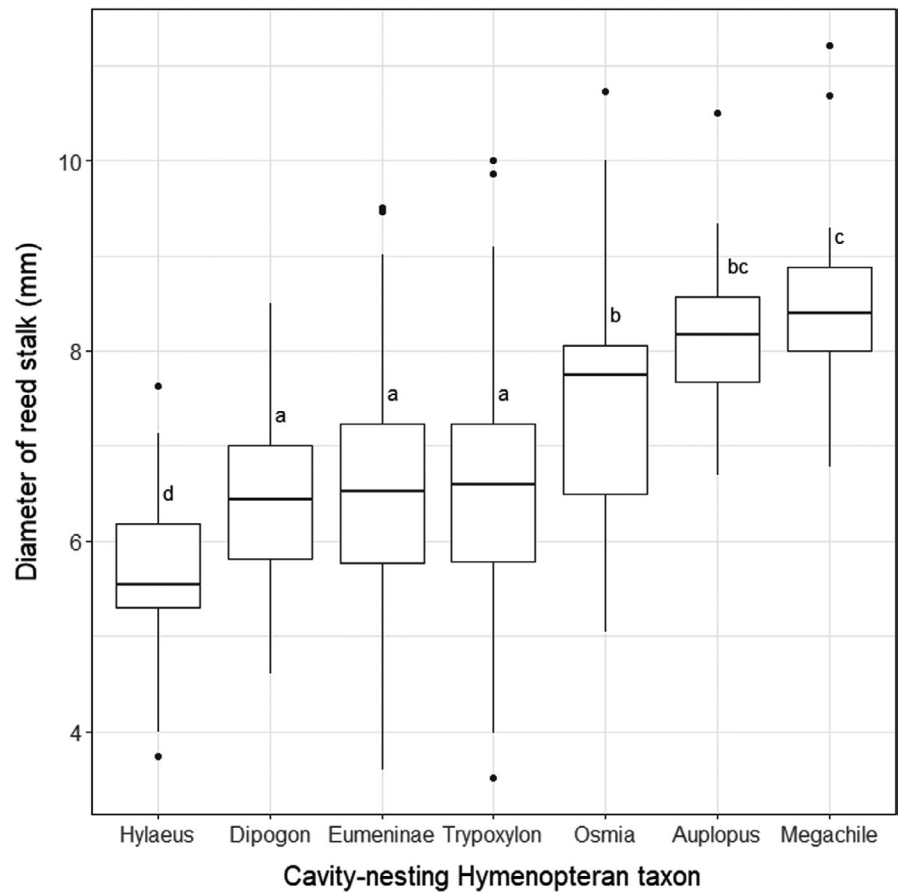
**TABLE 3** Results of generalized linear mixed models (GLMMs) assuming a Poisson distribution, testing for the relationship between the proportion and edge density of low-intensity agricultural areas within 250 m around the eight study sites and the total number of spider specimens per nest and site from families, which were most commonly preyed by the wasp genera *Trypoxylon* (Try) and *Dipogon* (Dip)

**TABLE 4** Results of linear models (LMs) testing for the relationship between the proportion and edge density of low-intensity agricultural areas within 250 m around the eight study sites and the Shannon's Diversity Indices (SDIs) per site of the Hymenopteran taxa and *Trypoxylon* spider prey

percentages of woody habitats, compared to sites with low percentages of woody habitats, and Fabian et al. (2013) also reported that forest cover had a positive effect on the species richness of wasps. All three studies were conducted in intensively managed agricultural landscapes with relatively low proportions of semi-natural habitats, which may explain the positive effect of an increasing proportion of semi-natural habitats on the Hymenopteran species diversity in their studies.

Regarding the spider prey of *Dipogon* and *Trypoxylon*, only the numbers of Thomisid prey specimens found in *Dipogon* nests were significantly affected by low-intensity agricultural areas, with an increasing proportion in the studied landscape sectors having a negative effect on the number of preyed specimens. An increasing proportion of low-intensity agricultural areas also had a significant effect on the diversity of spider prey found in the nests of *Trypoxylon*, with the diversity being higher at study sites surrounded by a higher proportion of low-intensity agricultural areas. In other words, the lower the proportion of low-intensity agricultural areas was around the study sites, the higher was the proportion of Araneid specimens among the spiders preyed by *Trypoxylon*, which resulted in a lower diversity of *Trypoxylon* spider prey. The highest numbers of Araneid prey were encountered at the study sites SV1 and SV3, where the proportion of low-intensity agricultural areas was the lowest with regards to all eight study sites (Table S1). Hoffmann et al. (2020), however, reported exactly the opposite, with an increasing area of grassland having a negative effect on the species diversity of spiders in *Trypoxylon* nests. Again, this contrasting finding may be explained by the different composition and structure of the intensively managed agricultural landscape in their study area, where they found that *Trypoxylon* mostly preyed in grassland patches. Therefore,

**FIGURE 5** Diameter of the reed stalks with nests for the seven cavity-nesting Hymenopteran taxa found at our study sites. The horizontal lines indicate the median value. The lower and upper whiskers represent the maximum values of the data that are within 1.5 times the interquartile range under the 25th and over the 75th percentile, respectively. Outlier values, indicated by black dots, are any values under or over this range. Same letters indicate no statistical differences between groups (Tukey's HSD test,  $p < 0.05$ )



**FIGURE 6** Principal component analysis (PCA) biplot of the numbers of *Trypoxylon* (Try) and *Dipogon* (Dip) spider prey per site. The length of the arrows represents the strength of the association with the study sites

they also assumed that a higher proportion of grassland may cause *Trypoxylon* specifically hunting for its preferred prey species, resulting in a lower prey diversity found in their nests.

## 5 | CONCLUSIONS

We encountered a considerably higher abundance of nests built by solitary wasps than solitary bees at all study sites. The two study sites with the highest numbers of solitary bee nests (=K3 and NV1) were both located the furthest away from the respective centers of the Natura 2000 protected areas. These results indicate that solitary bees are more common in areas, where the impact of human activities is stronger. In contrast to this, solitary wasps seem to rather avoid these areas. Our findings correspond well with those of similar previous studies from Western Europe, where solitary bees were the most abundant nest-building taxa in the majority of those studies, which were conducted in high-intensity agricultural areas. However, solitary wasps were the most abundant nest-building taxa in most studies, which were carried out in similar low-intensity agricultural or natural areas. Of course, this phenomenon could also be related to the chosen time period for sampling. However, as most studies from Table 1 chose similar time periods for sampling (mostly

from April to October), this might not be the cause for the lower abundances of solitary wasps and higher abundances of solitary bees in high-intensity agricultural landscapes. Therefore, we suggest that future studies not only should put more effort into sampling in reference landscapes with low-intensity agriculture but also focus more on solitary wasp taxa, when sampling such an area. As there are only a few such landscapes in Europe still remaining and as the maintenance of Hymenopteran biodiversity is crucial for the well-functioning of many ecosystem processes, our results can serve as a reference for future research in other areas, which are either less or more strongly influenced by humans.

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## CONFLICT OF INTEREST

The authors of this article have no financial or other conflict of interest to declare.

## AUTHOR CONTRIBUTIONS

**Károly Lajos:** Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (supporting); Methodology (equal); Supervision (equal); Validation (lead); Visualization (lead); Writing-original draft (lead); Writing-review & editing (lead). **Imre Demeter:** Conceptualization (supporting); Investigation (lead); Methodology (equal); Resources (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Róbert Mák:** Investigation (supporting). **Adalbert Balog:** Funding acquisition (lead); Project administration (supporting); Writing-original draft (supporting); Writing-review & editing (supporting). **Miklós Sároszpataki:** Conceptualization (lead); Funding acquisition (lead); Methodology (equal); Project administration (lead); Resources (equal); Supervision (equal); Writing-original draft (supporting); Writing-review & editing (supporting).

## DATA AVAILABILITY STATEMENT

All data generated or analyzed during this study were collected by the authors of this publication. The data that support the findings of this study are available in the Supplementary Information of this article. Additional data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.cjsxksn64>.

## COMPLIANCE WITH ETHICAL STANDARDS

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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