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Środowiskowa rola drzewostanów rosnących na gruntach porolnych w kształtowaniu zgrupowań roztoczy Mesostigmata (Acari, Mesostigmata)

Environmental role of stands growing on post-agricultural lands in forming the Mesostigmata mites (Acari, Mesostigmata) communities

Rozprawa doktorska w dziedzinie nauk rolniczych
w dyscyplinie nauki leśne
Doctoral thesis in agricultural sciences
in the forestry science discipline

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Streszczenie

Znaczące zwiększenie lesistości Polski jest możliwe dzięki zalesianiu gruntów porolnych, praktykowanemu w całej Europie. Problematyka tego działania polega w dużej mierze na specyficznych uwarunkowaniach fizyko-chemicznych i zubożeniu biologicznemu tych gruntów, jako konsekwencji długotrwałej uprawy rolnej. Badania nad strukturą fauny glebowej zasiedlającej grunty porolne były prowadzone w Europie przez innych badaczy, ale tylko niewielka liczba badań powiązała swoje wyniki z pełnym spektrum czynników środowiskowych, działających na opisywane struktury edafonu. Dodatkowo, wykorzystanie drapieżnych roztoczy z rzędu Mesostigmata, jako bioindykatorów sukcesji leśnej na gruntach porolnych, należy do wyjątkowej rzadkości. Niniejsze badania objęły różnowiekowe (22, 42 i 62-letnie), jednogatunkowe drzewostany sosny zwyczajnej (*Pinus sylvestris* L.), dębu bezszypułkowego (*Quercus petraea* (Matt.), brzozy brodawkowatej (*Betula pendula* Roth.), lipy drobnolistnej (*Tilia cordata* Mill.) i buka zwyczajnego (*Fagus sylvatica* L.) na gruntach porolnych i leśnych. W każdym z badanych wariantów siedliskowo-drzewostanowych określono typ gleby, dane taksacyjne drzewostanów oraz szeroki zakres parametrów fizyko-chemicznych gleby. W ciągu dwóch lat (2020, 2021) przeprowadzono cztery zbiory prób glebowych, których całkowita suma wyniosła 2056. Dzięki temu opracowano wyniki z 21 drzewostanów i 57 poletek badawczych. W ten sposób zaklasyfikowano łącznie 8484 roztoczy z rzędu Mesostigmata, należących do 77 taksonów. Badania wskazały, iż zgrupowania tych roztoczy, zasiedlające grunty porolne, są uboższe pod względem zagęszczenia, bogactwa gatunkowego i różnorodności gatunkowej od tych obecnych na gruntach leśnych, ale efekt ten zanika wraz z wiekiem drzewostanu. O różnicach tych decyduje między innymi zawartość sodu, azotu, cynku czy manganu w glebie. Ponadto udowodniono, że wpływ gatunku drzewa na zgrupowania roztoczy jest zależny od historii użytkowania terenu, dlatego w procesie rekultywacji gleb porolnych istotny staje się odpowiedni dobór składu gatunkowego drzewostanów. Dodatkowo udowodniono, że porównywanie wpływu gatunków drzew tworzących drzewostany na gruntach porolnych na zasiedlającą je faunę glebową, powinno odbywać się z uwzględnieniem zmian pór roku. Wynika to ze zmiennego wpływu konkretnego gatunku drzewa na warunki panujące w dnie lasu wraz ze zmianą warunków klimatycznych w cyklu rocznym.

Słowa kluczowe: Acari, grunty porolne, Mesostigmata, różnorodność biologiczna, zalesienia,

Abstract

A significant increase in Poland's forest cover has been achieved through afforestation of former agricultural land, which is practised throughout Europe. The problem of this treatment is largely due to the conditions of physical and chemical conditions and the biological impoverishment of such land as a consequence of long-term agricultural cultivation. Studies on the structure of soil fauna inhabiting post-agricultural land have been carried out in Europe by other authors, but only a small number of studies have related their results to the full spectrum of factors affecting that structures. Furthermore, the use of predatory predatory mites of the order Mesostigmata as bioindicators of forest succession on post-agricultural land is extremely rare in Europe. Our study included multi-aged (22-, 42- and 62-year-old), pure stands of Scots pine (*Pinus sylvestris* L.), sessile oak (*Quercus petraea* (Matt.), silver birch (*Betula pendula* Roth), small-leaved lime (*Tilia cordata* Mill.) and common beech (*Fagus sylvatica* L.) on post-agricultural and forest land. Soil type, stand taxation data and a wide range of soil physico-chemical parameters were identified in each of the habitat and stand variants studied. After two years of sample collection, results from 21 stands and 57 study plots were compiled. In this way, a total of 8484 individuals of mites of the order Mesostigmata, belonging to 77 taxa, were described. As a result, it was shown that the groups of these mites inhabiting post-agricultural lands are poorer in abundance and diversity than those present on forest land, but that this effect disappears with the age of the stand. These differences are determined, among other things, by the content of sodium, nitrogen, zinc or manganese in the wider soil. Furthermore, it has been proven that the influence of tree species on mite assemblages is dependent on the history of land use, so it becomes important to select an appropriate tree stand species composition when rehabilitating post-agricultural soils. In addition, it has been shown that a comparison of the influence of tree species in post-agricultural stands on the soil fauna should take into account seasonal changes. This is due to the changing influence of a particular tree species on forest floor conditions as climatic conditions change over the annual cycle.

Key words: Acari, afforestation, biodiversity, Mesostigmata, post-agricultural lands

1. Wstęp

Drzewostany rosnące na gruntach porolnych są obecne w całej Europie (De Frenne i in., 2011), zarówno jako efekt celowego zalesiania, jak i spontanicznej naturalnej sukcesji (Krawczyk, 2015; Fayet i in., 2022). W Polsce zalesianie gruntów porolnych było prowadzone na szeroką skalę w drugiej połowie XX wieku, ze szczególnym uwzględnieniem lat 60. oraz ostatniej dekady minionego stulecia i wprowadzonego wówczas Krajowego Programu Zwiększania Lesistości. Wiodący udział w tym procesie miały grunty rolne o najmniejszej wartości użytkowej (Kaliszewski, 2016). W rezultacie w latach 1945-2016 lesistość Polski wzrosła z 20,8% do 29,6% (Krawczyk, 2021). Historia użytkowania gruntów rolnych obejmuje wylesianie i długotrwałą uprawę, które doprowadziły do poważnej degradacji gleby i zmniejszenia różnorodności biologicznej fauny glebowej (Ponge i in., 2013). O ile odradzanie się ekosystemu leśnego na gruntach porolnych w wyniku naturalnej sukcesji jest procesem długotrwałym i wieloetapowym, o tyle zalesianie tychże gruntów odbywa się w sposób uproszczony i kontrolowany (Krawczyk, 2015). Poprzez zwiększenie powierzchni leśnej, proces ten może mieć istotny wkład w łagodzeniu skutków zmian klimatu (Lawson i Michler, 2014), zapewniając równocześnie korzyści z funkcji środowiskotwórczych i ochronnych, zwiększając różnorodność biologiczną, chroniąc gleby przed erozją oraz regulując cykl hydrologiczny, czy obieg składników odżywczych (Pawson i in., 2013; Harta i in., 2020). Grunty porolne są uznawane za trudne do zalesienia ze względu na ogół oddziałujących na nie w przeszłości czynników, jak i szereg odzwierciedlających ich działanie- cech fizycznych, chemicznych i biologicznych gleby (Szujecki, 1990; Scheu & Schulz, 1996; De Schrijver i in., 2012). Dokonane wylesienie pozbawiło omawianą glebę obecności systemów korzeniowych drzew, prowadząc do ograniczenia występowania ligniny i wydzielin korzeniowych, kluczowych dla jej leśnego charakteru. Ich obecność determinuje bowiem biodegradację próchnicy (Gorzelak, 1996; Yang i in., 2021) i utrzymuje specyficzne mikrośrodowisko (Sahani & Behera, 2001; Hinsinger i in., 2015; Xiao i in., 2024), w którym gleba oraz organizmy glebowe i systemy korzeniowe drzew są ze sobą współzależne (Heiniger i in., 2015). W takich okolicznościach, mikroorganizmy rozkładające ligninę zanikają, zaś bakterie rozkładające celulozę z roślin zielnych występują licznie (Krawczyk, 2021). Powtarzająca się w przeszłości na gruntach rolnych orka jest natomiast odpowiedzialna za ostateczne przekształcenie profilu glebowego, a cyklicznie nawożenie za modyfikację parametrów chemicznych gleby (Gorzelak, 1996; Rosenzweig i in., 2016; Renčo i in., 2020).

Odczyn gleby na gruntach porolnych jest wyraźnie wyższy niż na leśnych, natomiast stosunek węgla do azotu ulega zmniejszeniu (Holubík i in., 2014; Krawczyk, 2021) mimo, że zwiększony dostęp do azotu zwiększa w określonych warunkach sekwestrację dwutlenku węgla przez rośliny (de Vries i in., 2014; Du i de Vries, 2018). Jak wykazują liczne badania, akumulacja azotu w glebie jest jednym z czynników istotnie ograniczających bioróżnorodność roślin i zwierząt między innymi poprzez intensyfikowanie konkurencji międzygatunkowej (Schlesinger, 2009; Schwede i in., 2018; Bobbink i in., 2022) oraz niekorzystny wpływ na niektóre gatunki grzybów ektomykoryzowych (Parrent i Vilgalys, 2007). W przebiegu zalesiania gruntów porolnych problematyczna jest także obecność warstwy płużnej, przez którą przenikanie wody i korzeni w głąb profilu glebowego jest utrudnione (Szujecki, 1990). Drzewostany rosnące w tak niesprzyjających warunkach narażone są na ataki grzybów patogenicznych, a w szczególności hubę korzeni (*Heterobasidion annosum* (Fr.) Bref. *sensu lato*) (Sobczak, 1990; Sierota, 2011).

Ze względu na specyfikę gruntów porolnych były one w przeszłości zalesiane przede wszystkim pionierskimi gatunkami drzew o szerokim zakresie tolerancji ekologicznej, takimi jak sosna zwyczajna (*Pinus sylvestris* L.) i brzoza brodawkowata (*Betula pendula* Roth.) (Sobczak, 1990, 1996). Tworzenie monokultur sosnowych w oparciu o domieszki brzozowe wiąże się jednak z wysokim zagrożeniem ze strony patogenów grzybowych i gradacji owadów, na co polscy badacze i leśnicy zwrócili szczególną uwagę w latach 90. XX wieku (Bernacki, 1990; Rykowski, 1990; Sobczak, 1996). W efekcie, znaczenia nabrała przebudowa tychże drzewostanów w sposób zgodny z typem siedliskowym lasu i w oparciu o gatunki liściaste, takie jak dąb bezszypułkowy (*Quercus petraea* (Matt.) Liebl.), buk zwyczajny (*Fagus sylvatica* L.), czy lipa drobnolistna (*Tilia cordata* Mill.) (Zachara, 2019), wprowadzane do tychże drzewostanów rębniami gniazdowymi (Miś & Rączka, 2004). Ostatecznie, każdy z wymienionych gatunków wywiera inny wpływ na tempo i przebieg rekultywacji gleby (Smal & Olszewska, 2008; De Schrijver i in., 2009, 2012; Thomaes i in., 2012). Proces ten jest w znacznym stopniu oparty na dekompozycji martwej materii (Tejada i in., 2009; Y. Zhao i in., 2022), a więc jej pochodzeniu i aktywności biologicznej fauny glebowej (Huhta, 2007; Augustyniuk-Kram & Kram, 2020; Urbanowski i in., 2021). Jak dowiedli Gergócs i in. (2015), skład gatunkowy, możliwości rozrodcze oraz struktura troficzna zgrupowań roztoczy z rzędu Oribatida (mechowce) jest pośrednio uzależniona od jakości ściółki. Co więcej, Kaneko i Salamanca (1999), badając proces rozkładu jednogatunkowej i mieszanej ściółki stwierdzili dodatnią zależność między utratą masy ściółki mieszanej a liczebnością kolonizującej ją fauny glebowej, przy odwrotnej zależności w przypadku ściółki jednogatunkowej. Badania nad różnorodnością biologiczną szeroko pojętej fauny glebowej, zasiedlającej glebę gruntów porolnych, były prowadzone w Europie przy wykorzystaniu takich organizmów jak bakterie (Bacteria) (Makeschin, 1994; Peña i in., 2016; Renčo i in., 2020), nicienie (Nematoda) (Háněl, 2010; Jackson, 2012; Jaffuel i in., 2018; Renčo i in., 2020), roztocze (Acari) (Scheu & Schulz, 1996; Gormsen i in., 2006; Delcourt i in., 2023), skoczogonki (Collembola) (Heiniger i in., 2015; Harta i in., 2020), czy owady (Insecta) (Makeschin, 1994), dżdżownice (Lumbricidae) (Sigurdsson & Gudleifsson, 2013) i większe stawonogi (Arthropoda) (Scheu & Schulz, 1996). Badania Delcourt i in. (2023) wskazują na mniejszą biomasę i aktywność biologiczną drobnoustrojów w glebach gruntów porolnych w porównaniu do gleb leśnych. Peña i in. (2016) zbadali zgrupowania nicieni zasiedlających grunty porolne i leśne, wskazując na większą liczebność nicieni żerujących na korzeniach roślin w przypadku gleb porolnych. Swoje wyniki wyjaśnili wyższą zawartością fosforu w tkankach roślin porastających nawożone w przeszłości grunty, czego konsekwencją była ich większa wartość odżywcza. Z kolei Harta i in. (2020), badając drzewostany dębu bezszypułkowego i robinii akacjowej (*Robinia pseudoacacia* L.) rosnące na gruntach porolnych i leśnych, odnotowali wyraźnie wyższą liczebność, bogactwo gatunkowe i różnorodność skoczogonków w przypadku gruntów leśnych. Scheu i Schulz (1996) dowiedli natomiast, że różnorodność roztoczy z rzędu Oribatida wzrasta wraz z akumulacją węgla w wierzchniej warstwie gleby, a jej kolonizacja przez te saprofagiczne roztocze dotyczy w pierwszym etapie przede wszystkim warstwy ścioły. Wśród wyżej wymienionych badań brakuje jednak informacji na temat zgrupowań roztoczy z rzędu Mesostigmata (Acari, Mesostigmata), występujących w różnych wariantach dominującego gatunku drzewa oraz wieku drzewostanu, wraz z odniesieniem ich zagęszczenia, bogactwa gatunkowego i różnorodności gatunkowej do poszczególnych parametrów glebowych.

Znaczenie roztoczy z rzędu Mesostigmata w procesie formowania się i właściwego funkcjonowania gleb leśnych wynika z kluczowej roli, jaką te organizmy pełnią w glebowym łańcuchu troficznym. Jako dominująca liczbowo grupa drapieżników glebowych regulują one zagęszczenie organizmów saprofagicznych z niższych poziomów troficznych, takich jak nicienie, skoczogonki, larwy owadów i inne roztocze (Koehler, 1999). Tym samym przyczyniają się do prawidłowego obiegu energii i składników odżywczych w glebach leśnych (Ruf & Beck, 2005), wywierając pośredni wpływ na dynamikę dekompozycji (Urbanowski i in., 2021). Ich własna wrażliwość fizjologiczna na zaburzenia zachodzące w glebie oraz zauważalne w ich liczebności i bioróżnorodności reakcje na wszelkie zmiany w liczebności innych grup troficznych, stanowiących ich pokarm sprawia, że znakomicie sprawdzają się w roli bioindykatorów antropopresji wywieranej na siedliska leśne (Kamczyc i in., 2019). Wobec powyższego, warto zwrócić szczególną uwagę na drapieżne roztocze glebowe w kontekście różnic występujących pomiędzy gruntami porolnymi a leśnymi, z uwzględnieniem różnych gatunków drzew oraz wieku drzewostanu. Dodatkowym aspektem powinno być powiązanie określonych różnic w zgrupowaniach roztoczy glebowych z parametrami fizyko-chemicznymi gleby.

2. Przegląd literatury

Zakres dotychczasowej wiedzy na temat środowiska glebowego gruntów porolnych oraz zasiedlających je organizmów glebowych został zrewidowany w oparciu o artykuły naukowe pozyskane z bazy danych ISI Web of Science. Wszystkie objęte przeglądem badania zostały zrealizowane w Europie w latach 1979–2020 roku. Ostatecznie wybranych zostało 15 publikacji z 13 państw (Belgia, Czechy, Dania, Francja, Wielka Brytania, Niemcy, Węgry, Islandia, Irlandia, Polska, Słowacja, Szwecja i Szwajcaria) dotyczących zgrupowań fauny glebowej zasiedlającej grunty porolne, podzielonych następnie na trzy kategorie: mikro-, mezo- i makrofaunę. Wspomniane badania objęły łącznie 18 gatunków drzew, głównie liściastych (łącznie 14 gatunków). Wśród nich najczęściej analizowano buk zwyczajny (*Fagus sylvatica* L.), dąb szypułkowy (*Quercus robur* L.) i dąb bezszypułkowy). Badania wykazały, iż gatunki drzew, w zależności od sposobu wcześniejszego użytkowania gruntów, wpływają na skład chemiczny gleby, skład gatunkowy runa leśnego, zawartość składników odżywczych w tkankach roślin oraz strukturę zgrupowań organizmów glebowych. Na przykład de la Peña i in. (2016) odnotowali wyższą zawartość fosforu w glebie i tkankach roślinnych oraz niższą zawartość potasu w glebie na gruntach porolnych, porównując je z 220. letnimi lasami liściastymi. Gleby te nie różniły się jednak pod względem całkowitej zawartości azotu i biomasy roślin.

Podczas przeglądu dostępnej literatury zauważono brak odpowiedniej referencji dla określenia wpływu poszczególnych gatunków drzew i historii użytkowania terenu. Opisywane badania analizowały bowiem przede wszystkim zgrupowania zasiedlające pojedyncze formy zadrzewień, drzewostany w niejednolitych fazach rozwoju lub porastające odmienne typy gleb. Ponadto, porównanie dla drzewostanów rosnących na glebach leśnych stanowiły niejednokrotnie niezalesione pola uprawne lub łąki.

Spośród wyżej wymienionych publikacji zaledwie sześć dotyczyło zgrupowań organizmów zaliczanych do mezofauny. Obejmowały one łącznie siedem gatunków drzew i osiem typów gleb, wśród których zabrakło popularnej w Polsce gleby rdzawej. Większość badań zostało opartych o wąski zakres analiz fizyko-chemicznych gleby, ograniczonych do odczynu oraz zawartości azotu i fosforu. Odczyn glebowy był z reguły bardziej zasadowy na gruntach porolnych. Analizowane parametry glebowe nie były jednak używane w modelach statystycznych zawierających dane o liczebności, bogactwie gatunkowym i różnorodności badanych grup organizmów, stanowiąc wyłącznie element opisu poletek badawczych.

Harta i in. (2020) porównali populacje skoczogonków zasiedlających dojrzały drzewostan dębu bezszypułkowego, pole uprawne oraz 20. letnią plantację robinii akacjowej (*Robinia pseudoacacia* L.), której wprowadzenie na grunty porolne zostało poprzedzone kontrolowanym nawożeniem. Zgodnie z przewidywaniami, zgrupowania skoczogonków były najliczniejsze i najbardziej różnorodne gatunkowo w przypadku drzewostanu dębu bezszypułkowego, zaś najmniej w przypadku pola uprawnego.

Zgrupowania roztoczy glebowych zostały przebadane w zaledwie trzech spośród wyżej wymienionych prac (Scheu i Schulz, 1996; Gormsen i in., 2006; Keith i in, 2012). Scheu i Schulz (1996) skupili się wyłącznie na roztoczach z rzędu Oribatida, badając strukturę ich zgrupowań na różnych etapach sukcesji leśnej po wprowadzeniu buka zwyczajnego na gleby obsiewane wcześniej pszenicą. Gormsen i in. (2006) zbadali wpływ aktywnych zabiegów agrotechnicznych, spontanicznej wtórnej sukcesji oraz wprowadzenia różnych kompozycji roślinnych na gruntach porolnych na zgrupowania roztoczy glebowych z rzędów Oribatida, Astigmata, Prostigmata i Mesostigmata, opisując dla ostatniego z nich wyłącznie zagęszczenie. Keith i in. (2012) porównali bogactwo gatunkowe siedmiu grup organizmów (bakterie, grzyby, grzyby endomykoryzowe, nicienie, roztocze (bez określenia rzędu), dżdżownice i mrówki) w odniesieniu do pięciu typów siedlisk na terenie Irlandii. W żadnej z wymienionych wyżej publikacji roztocze z rzędu Mesostigmata nie stanowią roli bioindykatora sukcesji leśnej na gruncie porolnym. Brakuje ponadto prac w pełniejszym stopniu określających udział szerokiego zakresu czynników fizyko-chemicznych na dynamikę tego procesu w kontekście zgrupowań mezofauny glebowej.

Opisane powyżej publikacje posłużyły do opublikowania pracy przeglądowej, stanowiącej załącznik do niniejszej rozprawy doktorskiej.

3. Cel i hipotezy

Celem badań było rozpoznanie różnic w zagęszczeniu, bogactwie gatunkowym i różnorodności gatunkowej zgrupowań roztoczy z rzędu Mesostigmata (Acari, Mesostigmata = Gamasida) zasiedlających glebę różnowiekowych drzewostanów jednogatunkowych sosny zwyczajnej, dębu bezszypułkowego, brzozy brodawkowatej i lipy drobnolistnej, rosnących na gruntach porolnych i leśnych oraz poznanie wpływu poszczególnych parametrów chemicznych gleby na strukturę tych zgrupowań. Badanie wykonano w ramach trzech zaplanowanych eksperymentów w latach 2021 – 2022 na terenie Nadleśnictwa Opole.

Podjęte badania służyły weryfikacji trzech głównych hipotez badawczych:

Hipoteza 1: Zagęszczenie, bogactwo gatunkowe i różnorodność gatunkowa zgrupowań akarofauny glebowej z rzędu Mesostigmata, zasiedlającej wierzchnią warstwę gleby, są zależne zarówno od gatunku drzewa, jak i wcześniejszego sposobu użytkowania gruntu.

Uzasadnienie: Badania nad mezofauną zasiedlającą grunty porolne i leśne, prowadzone przez takich badaczy jak Scheu and Schulz (1996), Gormsen i in. (2006), Delcourt i in. (2023), Harta i in. (2020), czy Heiniger i in. (2015) dowodzą wyraźnych różnic w składzie gatunkowym i liczebności zgrupowań tych organizmów ze względu na historię użytkowania terenu. Za niższą bioróżnorodność i liczebność mezofauny glebowej gruntów porolnych odpowiada między innymi wyższy odczyn gleby i mniejsza akumulacja martwej materii (Harta i in., 2020). Wpływ poszczególnych gatunków drzew wynika z kolei między innymi z jakości akumulowanej pod nimi ściółki, co przekłada się na różnice w tempie dekompozycji i dostępności składników pokarmowych, a także z różnic w utrzymywaniu stabilnych warunków mikroklimatycznych i kształtowaniu składu gatunkowego runa leśnego (Zhao i in., 2014; Mueller i in., 2016; Frouz, 2018; Rola i in., 2021; Urbanowski i in., 2021). Jak dowiódł Kamczyc i in (2019), porównując zbiorowiska roztoczy z rzędu Mesostigmata w ściole siedmiu gatunków drzew liściastych (klon zwyczajny *Acer platanoides* L., k. jawor *A. pseudoplatanus* L., grab zwyczajny *Carpinus betulus* L., buk zwyczajny, lipa drobnolistnadąb szypułkowy, dąb czerwony *Q. rubra*) i czterech iglastych (jodła pospolita *Abies alba* Mill., modrzew europejski *Larix decidua* Mill., świerk pospolity *Picea abies* [L.] Karst., sosna zwyczajna), bogactwo gatunkowe i różnorodność roztoczy jest mniej zależna od gatunku ścioły niż ich liczebność, która była najwyższa w ściole jodły zwyczajnej, sosny pospolitej i dębu czerwonego.

Co ciekawe, liczebność zgrupowań tych roztoczy w przypadku drzewostanów sosnowych spadała wraz ze stopniem rozkładu martwej materii. Odrębną kwestią jest wpływ poszczególnych gatunków drzew na rekultywację gleby, a więc stopniowe przywracanie jej właściwości do stanu sprzed wylesień (Helmisaari i in., 2007; De Schrijver i in., 2009; Favas i in., 2016; Pietrzykowski, 2019). Efekt ten powinien znaleźć odzwierciedlenie w bogactwie gatunkowym roztoczy glebowych, w tym Mesostigmata (Ruf & Beck, 2005; Delcourt i in., 2023).

Hipoteza 2: Różnice w parametrach chemicznych gleby oraz zagęszczeniu, bogactwie gatunkowym i różnorodności gatunkowej roztoczy z rzędu Mesostigmata pomiędzy gruntem porolnym a leśnym będą zanikać wraz z rosnącym wiekiem drzewostanów, zaś dynamika tego procesu będzie różna ze względu na dominujący w drzewostanie gatunek drzewa.

Uzasadnienie: Grunty porolne były w przeszłości zalesiane głównie sosną zwyczajną jako gatunkiem drzewa o charakterze pionierskim. W dalszej kolejności do zalesień tychże gruntów używano również dębu (*Quercus* spp.) (Bernacki, 1990). Dotychczasowe badania wykazały, iż oba te rodzaje drzew mają nieco inny wpływ na wierzchnią warstwę gleby. Jest to, między innymi, efekt różnej akumulacji węgla w warstwie dna lasu (Vesterdal i in., 2002; Podrázský i in., 2009; Cukor i in., 2017). Może to wynikać nie tylko ze zróżnicowania ilościowego i jakościowego ścioły drzew, ale także z odmiennej dostępności światła w dnie lasu. Tym samym, w odmienny sposób kształtowany jest skład podszytu i roślin runa, które wpływają zarówno na zawartość materii organicznej w glebie, jak i warunki wilgotnościowe gleby, czy jej zasobność w składniki pokarmowe (Zhao i in., 2014; Mueller i in., 2016; Rola i in., 2021). Efekt ten, a także inne zmiany fizyko-chemiczne, są również zależne od wieku drzewostanu (Emborg, 1998; Clark & Johnson, 2011). W konsekwencji, zarówno gatunek drzewa (Kamczyc i in., 2019), jak i wiek drzewostanu (Migge i in., 1998) kształtują warunki siedliskowe dla gatunków tworzących zgrupowania organizmów glebowych, w tym roztoczy Mesostigmata. Przykładowo, Delcourt i in. (2023) wykazali, że wpływ historii użytkowania gruntów rolnych na zagęszczenie mikrostawonogów zależy od warunków pedoklimatycznych i maleje wraz z wiekiem drzewostanów.

Hipoteza 3: Zagęszczenie, bogactwo gatunkowe i różnorodność gatunkowa roztoczy glebowych oraz udział ich poszczególnych stadiów rozwojowych w zgrupowaniach będzie zależny od pory roku.

Uzasadnienie: Warunki środowiskowe, kształtujące zgrupowania mezofauny glebowej, w znacznej mierze zależą od temperatury i wilgotności w dnie lasu. Spadek wilgotności i wzrost temperatury powinien ograniczać zagęszczenie roztoczy glebowych (Salmane, 2000; Kamczyc i in., 2022). Także relacja poszczególnych stadiów rozwojowych jest zależna od pory roku i warunków klimatycznych, bowiem stadia młodociane – larwy, protonimfy i deutonimfy – są słabiej sklerotyzowane, będąc tym samym bardziej wrażliwymi na wzrost temperatury i utratę wody (Huhta & Hänninen, 2001). W związku z powyższym, ich udział w zgrupowaniach powinien być niższy latem i wzrastać w okresach o umiarkowanej temperaturze i większej wilgotności wierzchniej warstwy gleby, tj. na wiosnę i jesienią. Także wpływ gatunku drzewa na fluktuacje w składzie gatunkowym i zagęszczeniu roztoczy powinien ulegać zmianie wraz ze zmianą pory roku. Na przykładzie sosny zwyczajnej, lipy drobnolistnej i brzozy brodawkowatej efekt ten można wytłumaczyć najwyższą zdolnością pochłaniania wody przez ściółkę sosnową jesienią (Zhou i in., 2018), z największymi spadkami jej wilgotności w miesiącach suchych, co wynika z wyższego stosunku C:N (Ilek i in., 2024). Z kolei drzewostany brzozowe w ograniczony sposób chronią gleby przed nagrzewaniem i wysychaniem (Jonczak i in., 2020), podczas gdy lipa wyróżnia się takim właśnie oddziaływaniem (Rahman i in., 2017).

W każdej z opublikowanych prac przyjęto hipotezy szczegółowe, odnoszące się bezpośrednio do analizowanego układu doświadczalnego.

4. Materiały i metody

4.1. Teren badań

Badania terenowe zostały przeprowadzone w latach 2021-2022 na terenie Nadleśnictwa Opole (50°49'51.4"N 17°26'25.9"E). Obszar ten został wybrany ze względu na wielkoobszarowe zalesienia gruntów rolnych, przeprowadzone głownie w latach 90. XX wieku. Wszystkie powierzchnie są jednorodne pod względem rodzaju gleby i właściwości geologicznych. Wybrany do badań obszar obejmuje kompleks leśny Dąbrowa o powierzchni 5479,07 ha. Biorąc pod uwagę wilgotność gleby, lasy są zdominowane przez siedliska świeże (57% powierzchni), wilgotne (40%) i bagienne (3%). Średnia roczna suma opadów wynosi 603 mm, natomiast średnia roczna temperatura osiąga 8°C. Sezon wegetacyjny trwa 227 dni.

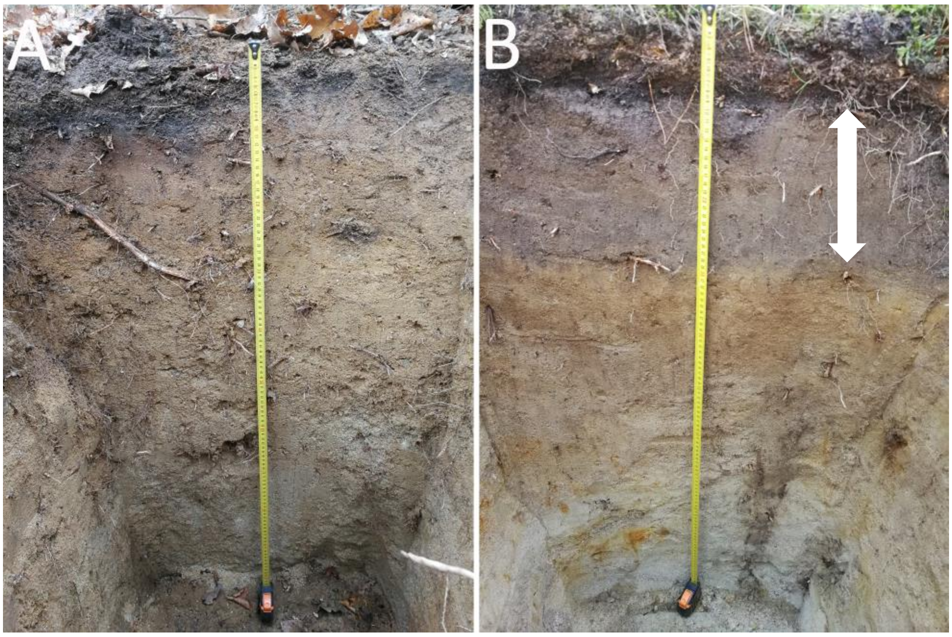
Pokrycie obszaru Nadleśnictwa roślinnością leśną wynosi około 17%. Sosna zwyczajna jest dominującym gatunkiem drzew leśnych, stanowiącym 73% powierzchni i udziału zasobów drzewnych. Przeciętny wiek drzewostanów wynosi 62 lata, a przeciętna miąższość drzewostanów 313 m^3/ha. Warstwa krzewów składa się głównie z kruszyny pospolitej (*Frangula alnus* Mill.), jarzębu pospolitego (*Sorbus aucuparia* L.), czeremchy zwyczajnej (*Prunus padus* L.) i świerka pospolitego, podczas gdy dno lasu pokrywają głównie takie gatunki jak: borówka czarna (*Vaccinium myrtillus* L.), trzcinnik leśny (*Calamagrostis arundinacea* (L.) Roth.), orlica pospolita (*Pteridium aquilinum* (L.) Kuhn) oraz mchy, takie jak: rokietnik pospolity (*Pleurozium schreberi* (Willd. ex Brid.) Mitt.)) i płonnik jałowcowaty (*Polytrichum juniperinum* Hedw). Przedział wysokościowy obszaru wynosi od 145 do 190 m n.p.m. (Plan Urządzenia Lasu dla Nadleśnictwa Opole, 2014). Gleby na badanym obszarze są zdominowane przez gleby rdzawe (Arenosols wg IUSS Working Group WRB, (2022)) – 45,3%, które są najczęściej występującymi glebami w drzewostanach zarządzanych przez Lasy Państwowe w Polsce (Rutkowski i in., 2021).

4.2. Układ doświadczalny

Układ doświadczalny objął łącznie 21 drzewostanów jednogatunkowych, pięciu gatunków drzew: sosny zwyczajnej, brzozy brodawkowatej, dębu bezszypułkowego, buka zwyczajnego oraz lipy drobnolistnej w wieku 22, 42 i 62 lat. W pierwszym etapie prac w ramach każdego drzewostanu wyznaczono po trzy powierzchnie kołowe o powierzchni 0,02 ha. Na każdej z wyznaczonych powierzchni wykopany został profil glebowy o głębokości jednego metra (pogłębiony do dwóch metrów przy użyciu świdra glebowego), celem potwierdzenia historii użytkowania terenu oraz typu gleby. Dodatkowo, z każdego poletka pobrane zostały próby warstwy organicznej oraz warstwy mineralnej (ok. 200 g), służące dalszym analizom fizyko-chemicznym w laboratorium Katedry Botaniki i Siedliskoznawstwa Leśnego oraz Katedry Chemii Rolnej i Biogeochemii Środowiska Uniwersytetu Przyrodniczego w Poznaniu. W kolejnym etapie zrealizowano pobór prób glebowych, przeznaczonych do analiz zgrupowań roztoczy z rzędu Mesostigmata. Do tego celu użyto próbnika o średnicy 5 cm i głębokości 15 cm. Z każdego poletka zebrano po 9 prób. Zbiór prób do ww. analiz realizowano w lipcu i październiku, w latach 2021-2022 (**Tabela 1**).

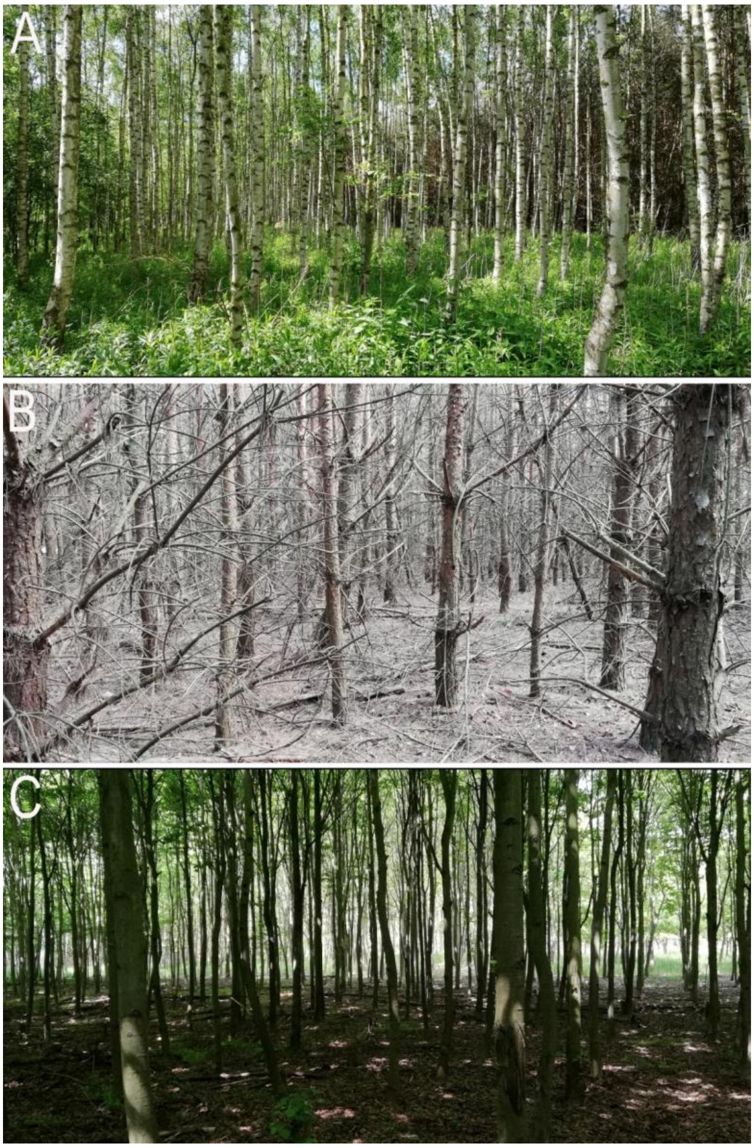
Układ badawczy obejmował następujące doświadczenia:

1. Wpływ drzewostanów sosnowych, dębowych i brzozowych w wieku 22 lat rosnących na gruncie porolnym i leśnym (**Rycina 1**) oraz drzewostanu bukowego na gruncie leśnym na właściwości fizyko-chemiczne gleby i roztocze z rzędu Mesostigmata. W ramach tego układu przeprowadzono trzy zbiory prób (lipiec 2021, 2022; październik 2021), w trakcie których z siedmiu poletek zebrano 567 prób glebowych przeznaczonych do analizy zoocenologicznej.
2. Wpływ drzewostanów sosnowych i dębowych w wieku 22, 42 i 62 lat (**Rycina 2**) na właściwości gleby i faunę glebową gruntów porolnych i leśnych. W tym układzie zebrano łącznie 1296 prób glebowych z 36 poletek w 4 powtórzeniach (lipiec 2021, 2022; październik 2021, 2022).
3. Wpływ 22. letnich drzewostanów sosnowych, brzozowych i lipowych (**Ryciny 3, 4**) na właściwości gleby i faunę glebową gruntów porolnych w ujęciu zmian pór roku. W ramach tego układu zebrano 288 prób z ośmiu poletek w czterech terminach (lipiec 2021, 2022; październik 2021, 2022).



Rycina 1.
Poglądowe porównanie profili glebowych na gruncie leśnym (A) i gruncie porolnym z widoczną warstwą płużną, oznaczoną białym wskaźnikiem (B) (Fot. K. Turczański).

Rycina 2.
Porównanie drzewostanów w różnym wieku: sosna zwyczajna w wieku 22 (A) i 62 (B) lat oraz dąb bezszypułkowy w wieku 22 (C) i 62 (D) lat (Fot. J. Malica).



Rycina 3.
Poletka badawcze na gruntach porolnych; wiek drzewostanów: 22 lata (lipiec 2021): A - drzewostan brzozowy, B - drzewostan sosnowy, C - drzewostan lipowy (Fot. J. Malica).

Rycina 4.
Strefa przejściowa pomiędzy 22. letnimi drzewostanami brzozy brodawkowatej i sosny zwyczajnej, porastającymi glebę rdzawą na gruncie porolnym (Fot. J. Malica).

Tabela 1.
Zestawienie podstawowych informacji o układach doświadczalnych.

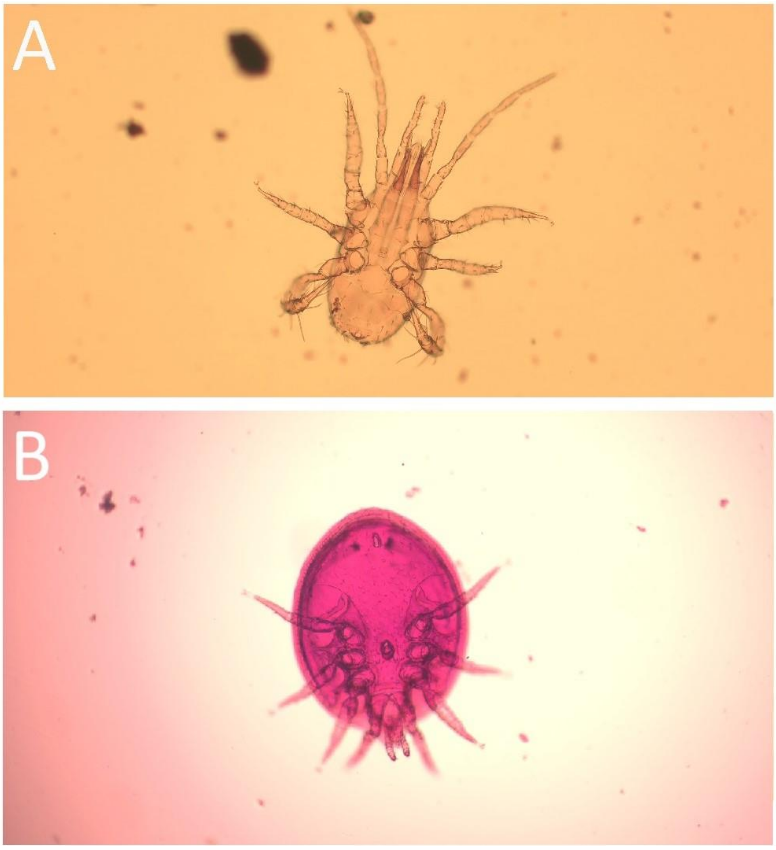
Numer doświadczenia	**Liczba poletek badawczych oraz prób**	**Gatunek drzew**	**Typ gleby**	**termin zbioru prób**
1	21 poletek 567 prób (+ 21 do analizy fizyko-chemicznej)	*P. sylvestris,* *B. pendula,* *Q. petraea,* *F. sylvatica*	grunt porolny grunt leśny	lipiec 2021, 2022 październik 2021
2	36 poletek 1296 prób (+ 36 do analizy fizyko-chemicznej)	*P. sylvestris,* *Q. petraea*	grunt porolny grunt leśny	lipiec 2021, 2022 październik 2021, 2022
3	8 poletek 288 prób (+ 8 do analizy fizyko-chemicznej)	*P. sylvestris,* *B. pendula,* *T. cordata*	grunt porolny	lipiec 2021, 2022 październik 2021, 2022

4.3. Zbiór danych

Faunę glebową wypłoszono z prób glebowych przy użyciu aparatu Berlesego-Tullgrena (**Rycina 5**), składającego się ze stałego źródła światła i źródła temperatury (żarówka 40W), a także z lejka oraz sitka o średnicy otworów 2 mm i pojemnika z alkoholem etylowym o stężeniu 75%. Cały proces przebiegał przez co najmniej sześć dni (przy stałej temperaturze wynoszącej na sitku 30,0 ± 0,5°C), aż do całkowitego wyschnięcia prób. W wyniku oddziaływania zmieniającego się gradientu wilgotności oraz temperatury fauna glebowa przemieszczała się z prób glebowych wprost do umieszczonych poniżej pojemników z alkoholem etylowym.

Po ukończonym etapie wypłaszania, spośród całej pozyskanej w tym procesie mezofauny glebowej, przy wykorzystaniu mikroskopu stereoskopowego oraz igły preparacyjnej, wyselekcjonowano roztocze z rzędu Mesostigmata. Roztocze te były utrwalane na szkiełku podstawowym w medium Hoyera, a w dalszej kolejności identyfikowane i klasyfikowane taksonomicznie na podstawie ich cech morfologicznych do rodzaju i/lub gatunku oraz stadium rozwojowego (**Rycina 6**). Identyfikacja roztoczy odbywała się przy użyciu mikroskopu (Zeiss AxioScope.A1) oraz specjalistycznych kluczy do oznaczania roztoczy z rzędu Mesostigmata, tj.: Micherdziński (1969), Giljarova i Bregetova (1977), Hirschmann i Wiśniewski (1982), Gwiazdowicz (2007), Kalúz i Fenda (2005), Karg (1971, 1993) oraz Mašán i Fenda (2004). Nazewnictwo oraz układ systematyczny rzędu Mesostigmata został przyjęty w publikacjach, stanowiących niniejszą rozprawę doktorską, za Błaszakiem (2008), Błoszykiem (2008) oraz Skorupskim (2008).

Rycina 5.
Aparat Berlesego-Tullgrena w trakcie wypłaszania fauny glebowej (fot. J. Malica).



Rycina 6.
Obraz mikroskopowy: (A) osobnika żeńskiego z gatunku *Veiagia nemorensis* oraz (B) osobnika męskiego z gatunku *Oodinychus ovalis* (C.L.Koch, 1839) (fot. J. Malica).

4.4. Analiza danych

Wartości bogactwa gatunkowego i różnorodności gatunkowej zostały przeliczone na wartości średnie wraz z podaniem błędu standardowego (ang. *Standard Error* – SE), w ramach przyjętych w doświadczeniach wariantów siedliskowo-drzewostanowych, terminu zbioru oraz poletka. Zebrane w ten sposób dane były analizowane przy użyciu klasycznych metod statystycznych, dostosowanych do wariantów przyjętych doświadczeń. Związek między czynnikami środowiskowymi a zagęszczeniem, bogactwem gatunkowym i różnorodnością gatunkową badanych zgrupowań roztoczy został przeanalizowany statystycznie przy użyciu odpowiednich modeli i testów statystycznych, w sposób zależny od rozkładu danych. W modelach przyjęto i zastosowano rozkład Tweedie`go. Ponadto, dla uzupełnienia analiz, wykorzystano uogólnione liniowe modele mieszane (ang. *generalized linear mixed models* – GLM) oraz liniowe modele mieszane (ang. *linear mixed models* – LMM), dopasowane do rozkładów uzyskanych danych. W celu określenia wpływu badanych czynników i różnic pomiędzy wariantami siedliskowo-drzewostanowymi, wszystkie modele zostały przetestowane za pomocą analizy wariancji (ANOVA) oraz testu Tukeya (*post-hoc*). Dodatkowo, celem określenia różnic i podobieństw pomiędzy badanymi zgrupowaniami roztoczy Mesostigmata, zasiedlającymi badaną ściółkę, przeprowadzono także kanoniczną analizę korespondencji (ang. *canonical correspondence analysis of principal coordinates* (CCA)) oraz analizę krzywych kumulacji bogactwa gatunkowego (ang. *cumulative species richness*) i analizy sieciowe (ang. *co-occurrence network for bipartite relationships*). Wszystkie analizy statystyczne wykonane zostały przy użyciu programu JMP Pro 13.0.0. (SAS Institute Inc. Cary, NC, USA; https://www.jmp.com) oraz oprogramowania R Studio (R Core Team R: A Language and Environment for Statistical Computing; https://www.Rproject.org/).

Analiza zoocenologiczna opracowanych danych objęła rozpoznanie struktury zgrupowań roztoczy w glebie różnogatunkowych i różnowiekowych drzewostanów na gruntach porolnych i leśnych oraz stopnia podobieństwa gatunkowego zgrupowań roztoczy w analizowanych siedliskach. Różnorodność zgrupowań roztoczy z rzędu Mesostigmata została obliczona na podstawie wskaźnika Shannona-Wienera (H′) o postaci:

$$H' = -\Sigma p_i \times \ln(p_i),$$

gdzie p_i to udział poszczególnych gatunków w zgrupowaniu roztoczy.

Wartość wskaźnika H′ rośnie wraz ze zwiększającą się liczbą gatunków w zbiorowisku oraz stopniem wyrównania ich liczebności. Jego wyższa wartość świadczy o większej stabilności funkcjonalnej analizowanego ekosystemu (Shannon i Weaver, 1963). Wskaźnik Shannona-Wienera jest jednym z najlepszych wskaźników, służących porównywaniu populacji organizmów funkcjonujących w ekosystemie, dostarczając wiarygodnego wyniku, bez względu na liczbę analizowanych prób (Odum, 1982). Największy wpływ na jego wartość mają gatunki występujące pospolicie w badanym środowisku, czyli dominujące w strukturze zgrupowania organizmów. Natomiast grupa gatunków o niewielkiej liczebności wywiera na tę wartość odwrotny wpływ (Madej, 2004).

5. Główne wyniki pracy

Wykazano, że zgrupowania roztoczy glebowych z rzędu Mesostigmata są kształtowane zarówno przez historię użytkowania terenu (grunty porolne *vs* grunty leśne), jak i skład gatunkowy drzewostanu, jego wiek oraz termin zbioru prób. Efekt działania każdego z tych czynników był zauważalny w zmianie zagęszczenia oraz bogactwa gatunkowego i różnorodności opisywanych zgrupowań (**Tabela 2**).

W ramach przeprowadzonych badań, opisano łącznie 8484 osobniki, sklasyfikowane jako 77 taksonów, należących do wspomnianego rzędu roztoczy (**Tabela 3**). Dominującymi gatunkami roztoczy były: *Veigaia nemorensis* (C.L. Koch) (13,92% wszystkich wykazanych osobników), *Zercon peltatus* C.L.Koch (12,45%) oraz *Paragamasus conus* (Karg) (7,73%). Zarówno pod względem wpływu historii użytkowania gruntu, jak i składu gatunkowego drzewostanu i jego wieku, największe różnice ujawniały się na poziomie bogactwa gatunkowego roztoczy, mniejsze zaś w przypadku ich zagęszczenia i różnorodności gatunkowej. Efekt zróżnicowania struktury zgrupowań roztoczy ze względu na historię użytkowania terenu był najwyraźniejszy w najmłodszych drzewostanach i zanikał wraz z ich wiekiem.

Tabela 2.
Główne wyniki doświadczeń przeprowadzonych w ramach rozprawy doktorskiej.

Badany parametr	**Doświadczenie 1**	**Doświadczenie 2**	**Doświadczenie 3**
Liczebność roztoczy	Liczebność całkowita: **1355 osobników** Największa liczebność została odnotowana w: ***B. pendula* – grunt leśny**	Liczebność całkowita: **6730 osobników** Największa liczebność została odnotowana w: **42-letni drzewostan *Q. petraea* –grunt porolny**	Liczebność całkowita: **399 osobników** Największa liczebność została odnotowana w: ***P. sylvestris* (październik)** ***T. cordata* (lipiec)**
Bogactwo gatunkowe	Drzewostan (gatunek drzewa) o największej wartości: ***Q. petraea* – grunt leśny**	Drzewostan (gatunek drzewa) o największej wartości: **62-letni drzewostan *Q. petraea* – grunt porolny**	Drzewostan (gatunek drzewa) o największej wartości: ***P. sylvestris* (październik)**
Różnorodność gatunkowa	Największa różnorodność została odnotowana w: ***Q. petraea* – grunt leśny**	Największa różnorodność została odnotowana w: **62-letni drzewostan *Q. petraea* – grunt porolny**	Największa różnorodność została odnotowana w: ***P. sylvestris* (październik)**
Dominujące gatunki roztoczy	***Veigaia nemorensis*** ***Zercon peltatus*** ***Paragamasus conus***	***Veigaia nemorensis*** ***Zercon peltatus*** ***Paragamasus conus***	***Veigaia nemorensis*** ***Hypoaspsis aculeifer***
Czynniki kształtujące zgrupowania roztoczy	Bogactwo gatunkowe: **zawartość sodu w ściole; historia użytkowania terenu; gatunek drzewa** Różnorodność gatunkowa: **zawartość sodu w ściole; historia użytkowania terenu**	Liczebność: **gęstość objętościowa; pH ścioły, zawartość azotu i sodu w ściole, zawartość cynku w glebie mineralnej** Bogactwo gatunkowe: **Zawartość manganu w glebie mineralnej**	Liczebność: **pora roku, zawartość żelaza w glebie mineralnej** Bogactwo gatunkowe: **pora roku, zawartość żelaza w glebie mineralnej, zawartość azotu w ściole** Różnorodność gatunkowa: **pora roku, zawartość żelaza w glebie mineralnej, zawartość azotu w ściole**

Tabela 3.
Lista wykazanych taksonów roztoczy z rzędu Mesostigmata, w doświadczeniach wykonanych w ramach niniejszej rozprawy doktorskiej. Obecność osobników danego gatunku oznaczono za pomocą symbolu +.

Lp.	**Takson**	**Doświadczenie 1**	**Doświadczenie 2**	**Doświadczenie 3**
1	*Alliphis halleri* (Canestrini & Canestrini, 1881)	+	+	+
2	*Amblyseius* spp.	+	+	+
3	*Antennoseius bacatus* Athias-Henriot, 1961	+	+	+
4	*Antennoseius bullitus* Karg, 1969	+		
5	*Arctoseius eremitus* (Berlese, 1918)		+	
6	*Arctoseius venustulus* (Berlese, 1917)		+	+
7	*Asca aphidioides* (Linnaeus, 1758)	+	+	
8	*Asca bicornis* (Canestrini & Fanzago, 1887)		+	
9	*Calaenopsis badius* (C.L.Koch, 1839)		+	
10	*Discourella modesta* (Leonardi, 1889)		+	
11	*Eugamasus cavernicolus* Trägårdh, 1912			
12	*Eviphis ostrinus* (C.L.Koch, 1836)	+	+	
13	*Gamasellodes bicolor* (Berlese, 1918)	+	+	+
14	*Geholaspis* spp.		+	
15	*Gamasellus montanus* (Willmann, 1936)			+
16	*Holoparasitus calcaratus* (C.L.Koch, 1839)	+	+	
17	*Holoparasitus rotulifer* (Willmann, 1940)		+	
18	*Hypoaspis aculeifer* (Canestrini, 1883)	+	+	+
19	*Hypoapsis karawaiewi* (Berlese, 1903)	+		
20	*Hyposapis praesternalis* (Willmann, 1949)	+	+	+
21	*Hypoaspis vacua* (Michael, 1891)	+	+	
22	*Hypoaspis* spp.	+	+	+
23	*Laelaspis astronomica* (C.L.Koch, 1839)	+	+	
24	*Lasioseius lawrencei* (Evans, 1958)	+	+	
25	*Leioseius elongatus* Evans, 1958	+	+	
26	*Leioseius* spp.		+	
27	*Leptogamasus* spp. (Trägårdh, 1936)	+	+	
28	*Leptogamasus succineus* Witaliński, 1973		+	+
29	*Leptogamasus suecicus* (Trägårdh, 1936)	+	+	
30	*Leptogamasus tectegynellus* (Athias Henriot, 1967)	+	+	+
31	*Macrocheles montanus* (Willmann, 1951)	+	+	+
32	*Macrocheles* spp.	+	+	+
33	*Olodiscus minima* (Kramer, 1882)	+	+	+
34	*Ololaelaps placentula* (Berlese, 1887)		+	
35	*Olopachys suecicus* (Sellnick, 1950)	+	+	
36	*Oodinychus ovalis* (C.L.Koch, 1839)	+	+	+
37	*Pachylaelaps bellicosus* (Berlese, 1920)	+	+	
38	*Pachylaelaps dubius* (Hirschmann&Krauss, 1965)		+	
39	*Pachylaelaps furcifer* (Oudemans, 1903)	+	+	
40	*Pachylaelaps ineptus* Hirschmann & Krauss 1965	+		
41	*Pachylaelaps longisetis* (Halbert, 1915)	+	+	
42	*Pachylaelaps* spp.		+	

Lp.	Takson	Doświadczenie 1	Doświadczenie 2	Doświadczenie 3
43	*Pachyseius humeralis* (Berlese, 1910)		+	+
44	*Paragamasus conus* (Karg, 1971)	+	+	+
45	*Paragamasus jugincola* (Athias Henriot, 1967)	+	+	+
46	*Paragamasus puerilis* (Karg, 1963)	+	+	
47	*Paragamasus runcatellus* (Berlese, 1903 sensu Karg, 1971)	+	+	+
48	*Paragamasus* spp.	+	+	+
49	*Paragamasus vagabundus* (Karg, 1968)	+	+	+
50	*Parazercon radiatus* (Berlese, 1914)		+	
51	*Pergamasus barbarus* (Berlese, 1904)	+	+	+
52	*Pergamasus crassipes* (Linnaeus, 1758)	+	+	+
53	*Pergamasus mediocris* Berlese, 1904			+
54	*Pergamasus septentrionalis* (Oudemans, 1902)	+	+	+
55	*Pergamasus* spp.	+	+	+
56	*Proctolaelaps juradeus* (Schweizer, 1949)	+	+	
57	*Prozercon kochi* (Sellnick, 1943)	+	+	
58	*Rhodacarellus silesiacus* (Willmann, 1936)		+	
59	*Rhodacarellus subterraneus* (Willmann, 1935)		+	
60	*Rhodacarus coronatus* (Berlese, 1921)	+	+	
61	*Rhodacarus mandibularis* (Berlese, 1921)	+	+	+
62	*Trachytes aegrota* (C.L.Koch, 1841)	+	+	+
63	*Trachytes montana* Willmann, 1953	+	+	
64	*Trachytes pauperior* (Berlese, 1914)		+	
65	*Urodiaspis tecta* (Kramer, 1876)	+	+	
66	*Uropoda* spp.	+	+	
67	*Veigaia cerva* (Kramer, 1876)	+	+	+
68	*Veigaia decurtata* (Athias Henriot, 1961)	+	+	+
69	*Veigaia exigua* (Berlese, 1916)	+	+	+
70	*Veigaia kochi* (Trägårdh, 1901)	+	+	
71	*Veigaia nemorensis* (C.L.Koch, 1839)	+	+	+
72	*Veigaia planicola* (Berlese, 1892)	+	+	+
73	*Vulgarogamasus kraepelini* (Berlese, 1904)	+	+	+
74	*Zercon hungaricus* (Sellnick, 1958)	+	+	+
75	*Zercon peltatus* C.L.Koch, 1836	+	+	+
76	*Zercon* spp.	+	+	
77	*Zercon triangularis* (C.L.Koch, 1836)	+	+	+

5.1. Wpływ historii użytkowania terenu i właściwości fizyko-chemicznych gleby na zgrupowania roztoczy z rzędu Mesostigmata (Acari, Mesostigmata), zasiedlające drzewostany na gruntach porolnych

Publikacja 1: Malica, J., Rączka, G., Turczański, K., Andrzejewska, A., Skorupski, M., Urbanowski, C.K. & Kamczyc, J. (2024). Impact of land use history and soil properties on soil mite communities (Acari, Mesostigmata) inhabiting stands growing on post-agricultural land. Land Degradation & Development, 35(5), 1776–1791. https://doi.org/10.1002/ldr.5020

Analiza cech fizyko-chemicznych gleby wykazała istotne statystycznie różnice pomiędzy badanymi siedliskami (grunt leśny *vs* grunt porolny), dotyczące takich parametrów jak: odczyn, zawartość materii organicznej, gęstość objętościowa, zawartość węgla organicznego oraz stężenia pierwiastków, takich jak potas, cynk, miedź, żelazo, mangan, sód, cynk oraz kadm. Na poziomie ogólnym gleby gruntów porolnych charakteryzowały się wyższym odczynem gleby, gęstością objętościową i zawartością manganu, zaś gleby gruntów leśnych były bardziej wilgotne i bogatsze w węgiel organiczny. Najniższe pH ściółki leśnej odnotowano w drzewostanie sosnowym na gruncie leśnym (4,24 ± 0,27). Co ciekawe, zawartość materii organicznej była najwyższa w drzewostanie dębowym na gruncie leśnym (4,86 ± 0,32%), a najniższa w drzewostanie dębowym na gruncie porolnym (1,93 ± 0,32). Ten sam wzorzec odnotowano dla zawartości węgla organicznego (odpowiednio 2,82 ± 0,19% i 1,12 ± 0,19%). Najmniejszą gęstość objętościową odnotowano w drzewostanach brzozowych na gruntach leśnych (0,75 ± 0,18 g/m^3). Z kolei najwyższą wilgotność gleby stwierdzono w drzewostanach brzozowych, rosnących na gruntach leśnych (9,99 ± 1,98%), a najniższą w drzewostanach sosnowych na gruntach porolnych (3,15 ± 0,37).

W ramach badań nad wpływem historii użytkowania terenu oraz warunków mikrosiedliskowych, kształtowanych przez drzewostany poszczególnych gatunków drzew (sosny zwyczajnej, brzozy brodawkowatej, dębu bezszypułkowego oraz buka zwyczajnego) i poszczególnych parametrów glebowych na zgrupowania roztoczy z rzędu Mesostigmata, opisano 1355 osobników, zidentyfikowanych jako 58 taksonów (50 gatunków i osiem rodzajów). Większość osobników sklasyfikowano do rodziny Parasitidae (348 osobników; 25% ogólnej liczby osobników, odpowiednio), Zerconidae (205; 15,1%) i Veigaiidae (189; 14,0%)

oraz gatunki *Veigaia nemorensis* (C.L. Koch) (165; 12,2%), *Zercon peltatus* C.L. Koch (156; 11,5%) i *Paragamasus conus* (Karg) (141; 10,4%). Tylko cztery opisane taksony występowały w każdym z siedmiu wariantów siedliskowo-drzewostanowym (sosny zwyczajnej, brzozy brodawkowatej, dębu bezszypułkowego oraz buka zwyczajnego na gruncie leśnym*;* sosny zwyczajnej, brzozy brodawkowatej oraz dębu bezszypułkowego na gruncie porolnym). Były nimi: *Hypoaspis aculeifer* (Canestrini), *P. conus*, *Paragamasus* spp. i *V. nemorensis*. Każdy z wyżej wymienionych gatunków jest typowy dla siedlisk leśnych, więc ich dominacja i stałość występowania nie jest zadziwiająca (Skorupski, 2008; Skorupski i in., 2013; Manu, 2014). Z kolei 17 innych gatunków pojawiło się tylko w jednym wariancie siedliskowo-drzewostanowym. Wartym zauważenia jest fakt, iż drugi najliczniej występujący gatunek *Zercon peltatus*, nie pojawił się w przypadku dwóch badanych siedlisk, drzewostanu dębowego oraz brzozowego na gruncie porolnym. Jest to gatunek nematofagiczny (Kamczyc i in., 2019) o wysokiej wrażliwości na metale ciężkie (Seniczak i in., 1997), który licznie występował na gruncie leśnym. Wskazuje to na powyższy gatunek, jako potencjalnie wartościowy bioindykator dawnej degradacji siedliska.

Analizy statystyczne wykazały, że zagęszczenie roztoczy było kształtowane przez historię użytkowania terenu oraz zawartość sodu w ściole, osiągając najwyższą wartość w drzewostanie brzozowym na gruncie leśnym (1888,89 ± 240,72 osobników/m^2). Największe różnice statystyczne występowały tu pomiędzy wymienionym powyżej wariantem a drzewostanem brzozowym i dębowym na gruncie porolnym, gdzie zagęszczenie roztoczy było najmniejsze (odpowiednio 672,84 ± 169,69 i 574,07 ± 109,75 osobników/m^2). Największe bogactwo gatunkowe zostało odnotowane w przypadku drzewostanu dębowego na gruncie leśnym (21,33 ± 2,73 gatunków), natomiast najniższe w drzewostanie dębowym na gruncie porolnym (9,33 ± 1,86). Ten parametr podlegał kształtowaniu ze strony trzech czynników siedliskowych: historii użytkowania terenu, zawartości sodu w ściole oraz dominującego gatunku drzewa. Dla porównania, różnorodność gatunkowa była, podobnie jak zagęszczenie, kształtowana tylko przez historię użytkowania terenu i zawartość sodu w ściole, osiągając najwyższą wartość w drzewostanie dębowym na gruncie leśnym, zaś najniższą w drzewostanie dębowym na gruncie porolnym. W przypadku bogactwa gatunkowego i różnorodności gatunkowej roztoczy wskaźniki te osiągały zarówno najwyższe, jak i najniższe wartości w drzewostanach dębowych. Głównym czynnikiem, różnicującym drzewostany dębowe, była historia użytkowania gruntu, który porastały. Wyraźna przewaga gruntów leśnych nad porolnymi pod względem zagęszczenia, bogactwa gatunkowego i różnorodności gatunkowej roztoczy z rzędu Mesostigmata, potwierdza przyjętą na potrzeby niniejszej rozprawy hipotezę, stanowiącą potwierdzenie tendencji opisywanych przez innych autorów. Jak zauważyli Aponte i in. (2012), specyfika fizyko-chemiczna gruntów porolnych może zaburzać proces dekompozycji martwej materii poprzez brak typowych dla lasów struktur grzybowych. To zaś, oddziałując na kolejne poziomy troficzne, ogranicza zagęszczenie i różnorodność zgrupowań drapieżnych roztoczy (Koehler, 1999; Schneider i in., 2005). Zgodnie z wynikami niniejszych badań, istotna dla struktury tych zgrupowań jest również zawartość sodu w ściole leśnej. Zjawisko to może znajdować swoje wytłumaczenie w wynikach badań Ji i in. (2020), którzy dowiedli, że umiarkowane zwiększenie stężenia sodu w glebie sprzyja dynamice dekompozycji oraz kolonizacji ścioły przez faunę glebową, poprzez ograniczenie efektu ang. „*Home Field Advantage*". Hipoteza ta zakłada, że autochtoniczna fauna glebowa jest lepiej przystosowana do lokalnych warunków panujących w danym mikrosiedlisku, w tym materiału organicznego zróżnicowanego pod względem składu gatunkowego roślinności tworzącego ściółkę (Horodecki i in., 2019). Ostatecznie, może to wyjaśniać efekt skrajnych wartości bogactwa gatunkowego i różnorodności w przypadku drzewostanów dębowych na gruntach o odmiennej historii użytkowania. Jak bowiem pokazują wyniki Marcosa i in. (2010), ścioła pochodząca z dębu jest uboższa w sód, niż ścioła sosnowa czy bukowa. W przypadku wzmożenia dekompozycji na gruntach o mniejszym bogactwie fauny glebowej może to mieć zatem kluczowe znaczenie (Ji i in., 2020).

5.2. Wpływ wieku drzewostanu dębu bezszypułkowego i sosny zwyczajnej na zgrupowania roztoczy zasiedlające grunty porolne

Publikacja 2: Malica, J., Urbanowski, C.K., Turczański, K., Rączka, G., Andrzejewska, A., Skorupski, M. & Kamczyc, J. (2024). Environmental role of different-aged pine and oak stands growing on post-agricultural and forest lands in forming the Mesostigmata mites communities. Land Degradation & Development, 1–20. https://doi.org/10.1002/ldr.5265

Badania przeprowadzone w różnowiekowych (22, 42 i 62 lata) drzewostanach dębu bezszypułkowego i sosny zwyczajnej, rosnących na gruntach porolnych i leśnych, wykazały istotne zmiany, zachodzące wraz z wiekiem drzewostanu w parametrach fizyko-chemicznych gleby. Należały do nich przede wszystkim: wzrost stosunku C:N w przypadku sosny i spadek w przypadku dębu oraz wspólny dla obydwu gatunków i typów gruntu spadek pH ścioły, który jednak był szczególnie widoczny na przykładzie drzewostanów sosnowych. Najniższą wartość pH ścioły odnotowano w 62. letnim drzewostanie sosnowym na gruncie porolnym (3,39 ± 0,05), zaś najwyższą w 22. letnim drzewostanie dębowym, także na gruncie porolnym (5,18 ± 0,15). W przypadku pH gleby mineralnej wiek drzewostanu nie był już tak znaczący, bowiem skrajne jego wartości odnotowano w 22. letnich drzewostanach dębowych: najniższą na gruncie leśnym (3,36 ± 0,10), a najwyższą na gruncie porolnym (4,33 ± 0,02).

W ramach analiz zgrupowań roztoczy z rzędu Mesostigmata opisano łącznie 6730 osobników, sklasyfikowanych jako 72 taksony (60 gatunków, 11 rodzajów i jedna rodzina). Większość roztoczy sklasyfikowano jako gatunki *Veigaia nemorensis* (C.L. Koch) (985 osobników; 14,64% wszystkich osobników), *Zercon peltatus* C.L. Koch (874; 12,99%), *Paragamasus conus* (Karg) (489; 7,27%) i *Rhodacarus coronatus* (Berlese) (481; 7,15%). W przypadku 31 opisanych gatunków ich udział w ogólnej liczbie wynosił mniej niż 10 osobników. Z kolei zaledwie osiem taksonów występowało we wszystkich badanych wariantach siedliskowo-drzewostanowych (*Hypoaspis aculeifer* (Canestrini), *Olodiscus minima* (Kramer), *Paragamasus conus*, *P. runcatellus*, *P. vagabundus*, *Paragamasus* spp., *Trachytes aegrota* oraz *V. nemorensis*). Co ciekawe, *R. coronatus* został wykazany w każdym drzewostanie, z wyjątkiem najmłodszych drzewostanów na gruntach porolnych. Jego liczebność wzrastała wraz z wiekiem drzewostanów na gruntach leśnych, natomiast na gruntach porolnych była najwyższa w drzewostanie 42. letnim. Podobnie *Rhodacarus mandibularis* Berlese i *Zercon hungaricus* (Sellnick) występowały wielokrotnie liczniej w młodych drzewostanach na gruntach leśnych niż na gruntach porolnych. W każdym wymienionym przypadku różnice te były mniej wyraźne w starszych drzewostanach.

Największe zagęszczenie roztoczy odnotowano w 42. letnim drzewostanie dębowym na gruncie porolnym (3847,22 ± 356,14 osobników/m^2), natomiast najniższą w 22. letnich drzewostanach sosnowym (685,19 ± 115,55) i dębowym (699,07 ± 104,20), na gruncie porolnym. Parametr ten był kształtowany przez gęstość objętościową i odczyn gleby, zawartość azotu i sodu w ściole oraz zawartość cynku w glebie mineralnej. Bogactwo gatunkowe osiągnęło najwyższą wartość w najstarszym drzewostanie dębowym na gruncie porolnym (32,33 ± 3,28 gatunków), a najniższą w najmłodszych drzewostanach dębowym (13,67 ± 1,76) i sosnowym (14,00 ± 1,15) na gruncie porolnym. Jak wykazały analizy, wskaźnik ten był kształtowany przez zawartość manganu w glebie mineralnej. Podobnie jak w przypadku bogactwa gatunkowego, najwyższą różnorodność gatunkową wykazano w najstarszym drzewostanie dębowym na gruncie porolnym (2,92 ± 0,08), natomiast najniższą w młodych drzewostanach złożonych z dębu (2,14 ± 0,13) i sosny (2,29 ± 0,03), rosnących na gruncie porolnym. Zarówno bogactwo gatunkowe, jak i różnorodność gatunkowa, wzrastały wraz z wiekiem w przypadku drzewostanu dębowego na gruncie porolnym. W przypadku drzewostanów sosnowych lub drzewostanów dębowych na gruncie leśnym nie wykazano takiej zależności.

Najniższe zagęszczenie roztoczy w najmłodszych drzewostanach dębowych i sosnowych, rosnących na gruntach porolnych, jest spójne z wynikami badań nad wpływem historii użytkowania gruntów na liczebność mezofauny glebowej, prowadzonymi przez takich badaczy jak Harta i in. (2020) oraz Delcourt i in. (2023). Najwyższe zagęszczenie w drzewostanach w średnim wieku (42 lata) można wytłumaczyć pozytywną reakcją fauny glebowej na trzebieże i wzrost dostępności światła w dnie lasu (Kamczyc i in., 2021). Ponadto Delcourt i in. (2023) odnotowali, że po 60 latach od zalesienia nie obserwowano już negatywnego wpływu wcześniejszego użytkowania gruntów na zgrupowania mikrostawonogów. Pod względem wpływu parametrów fizyko-chemicznych, wyniki badań stanowiących niniejszą rozprawę różnią się w pewnym stopniu od wyników Bedano i in. (2006), którzy wykazali dodatnią korelację między liczebnością roztoczy z rzędu Mesostigmata w glebie a gęstością objętościową i pH gleby. W naszym badaniu korelacja ta była bowiem ujemna w obu przypadkach. Badania Keshavarz i in. (2015) oraz Manu i in. (2019) wykazały z kolei, że zawartość cynku w glebie wpływa na różnorodność i bogactwo gatunkowe, ale nie na zagęszczenie roztoczy z rzędu Mesostigmata – odwrotnie, jak w przypadku wyników niniejszej rozprawy. Ponadto, badania przeprowadzone przez Cao i in. (2011) oraz Wierzbicką i in. (2019) nie potwierdziły pozytywnego wpływu azotu na zagęszczenie roztoczy w glebie.

5.3. Wpływ pory roku na zgrupowania roztoczy glebowych z rzędu Mesostigmata, zasiedlające jednogatunkowe drzewostany na gruncie porolnym

Publikacja 3: Malica, J., Urbanowski, C.K., Turczański, K., Rączka, G., Andrzejewska, A., Skorupski, M. & Kamczyc, J. (2025). Soil mite communities (Acari, Mesostigmata) in pure stands on post-agricultural lands: does season matter? Expperimental and Applied Acarology 94, 4. https://doi.org/10.1007/s10493-024-00

W ramach badań nad wpływem pory roku na zgrupowania roztoczy glebowych, zasiedlających grunty porolne, porównano ich zagęszczenie, bogactwo gatunkowe i różnorodność gatunkową w jednogatunkowych drzewostanach sosnowych, lipowych oraz brzozowych w lipcu i październiku. Łącznie wykazano 339 osobników, sklasyfikowanych jako 38 taksonów (33 gatunki i pięć rodzajów). Wyróżniono przy tym 266 samic i 50 samców oraz 83 stadia juwenilne. Najniższe uśrednione zagęszczenie roztoczy ze zbiorów przeprowadzonych w latach 2021 i 2022 opisane zostało w wariancie drzewostanu sosnowego i zbioru przeprowadzonego w lipcu (285 ± 115 osobników/m^2), zaś najwyższe w wariancie drzewostanu sosnowego i zbioru przeprowadzonego w październiku (1085 ± 270). Najniższe średnie bogactwo gatunkowe z dwóch lat zbiorów ponownie odnotowano w wariancie zbioru przeprowadzonego w lipcu w drzewostanie sosnowym (0,52 ± 0,20 gatunku), natomiast najwyższe w wariancie zbioru przeprowadzonego w październiku w drzewostanie sosnowym (1,37 ± 0,27). Najwyższą wartość wskaźnika różnorodności gatunkowej ponownie wykazano w próbach zebranych w październiku w drzewostanie sosnowym (0,40 ± 0,10), zaś najniższą w lipcu, również w drzewostanie sosnowym (0,12 ± 0,06).

Większość opisanych gatunków należała do rodzin Parasitidae (111 osobników), Laelapidae (95) i Veigaiidae (70). Najliczniej reprezentowanymi gatunkami były *Hypoaspis aculeifer* (86 roztoczy; 21,6% wszystkich wykazanych roztoczy, odpowiednio), *Veigaia nemorensis* (31; 7,8%) i *Trachytes aegrota* (C.L.Koch) (28; 7,0%). Każdy z tych gatunków występował najliczniej w drzewostanie lipowym w październiku. Tylko dwa gatunki występowały w każdym badanym wariancie: *Veigaia nemorensis* i *Hypoaspis aculeifer*. Aż 15 spośród opisanych gatunków występowało tylko w jednym drzewostanie. Zgodnie z posiadaną wiedzą, roztocze z rodziny Parasitidae występują we wszystkich typach lasów, a także na łąkach, torfowiskach i polach uprawnych. Są obecne przede wszystkim w ściółce i warstwie próchnicznej. Ich głównymi ofiarami są skoczogonki oraz inne roztocze, takie jak Oribatida i Astigmata. Z kolei rodzina Laelapidae obejmuje między innymi duże drapieżne gatunki z rodzaju *Hypoaspis* spp. Jego przedstawicielem jest *Hypoaspis aculeifer*, będący pospolitym gatunkiem pionierskim, występującym również licznie na gruntach porolnych (Skorupski, 2008). Do rodziny Veigaiidae należą gatunki wyspecjalizowane w żerowaniu na skoczogonkach, zasiedlające głównie ściółkę leśną, ale występujące także na łąkach i gruntach rolnych. Wraz z roztoczami z rodziny Parasitidae tworzą dominującą grupę drapieżników z rzędu Mesostigmata (Błoszyk, 2008; Skorupski, 2008). *Veigaia nemorensis* także jest gatunkiem powszechnym na gruntach porolnych, a nawet na terenach zdegradowanych lub poprzemysłowych (Skorupski i in., 2013). Kolonizuje głównie górne warstwy gleby: próchnicę organiczną i ściółkę. *Veigaia nemorensis*, w przeciwieństwie do ogólnej cechy rodziny Veiigaidae, żeruje głównie na gatunkach nicieni bakteriofagicznych i żywiących się korzeniami roślin (Manu i in., 2017).

Podsumowując, w badaniach stanowiących niniejszą rozprawę wykazano znacznie wyższe zagęszczenie roztoczy w październiku niż w lipcu, na przestrzeni dwóch lat zbiorów. Jest to zgodne z wynikami innych badań (Fujii & Takeda, 2017) i przyjętych przez nas hipotez, bowiem głównym czynnikiem regulującym liczebność roztoczy glebowych jest wilgotność i temperatura (Kaczmarek i in., 2011; Kamczyc i in., 2022). W warunkach klimatycznych Polski niższą liczebność w lipcu można wytłumaczyć wyższą temperaturą i szybko malejącą wilgotnością gleby latem, co powoduje spadek zagęszczenia roztoczy. Wraz z końcem lata temperatura pozostaje wysoka, ale wilgotność gleby wzrasta, co w efekcie powoduje wzrost zagęszczenia roztoczy w glebie (Wośc, 1999; Salmane, 2000). Ta sama zależność dotyczyła również bogactwa gatunkowego i różnorodności gatunkowej. Podobne znaczenie opadów i temperatury dla struktury zgrupowań roztoczy glebowych z rzędu Mesostigmata wykazali również Kamczyc i in. (2022), według których średni udział osobników dorosłych w całym zgrupowaniu roztoczy wzrastał jesienią, podczas gdy udział osobników młodocianych wzrastał latem. Zarówno latem, jak i jesienią udział samców był najniższy, a udział samic najwyższy. Interesującym wynikiem niniejszych badań był wzrost udziału młodych stadiów rozwojowych latem. Są one bowiem uważane za bardziej wrażliwe na wzrost temperatury i spadek wilgotności, co wiąże się z niższym stopniem sklerotyzacji ciała (Huhta & Hänninen, 2001). Osobniki dorosłe powinny być jednocześnie bardziej odporne na podobne fluktuacje pogodowe (Urbanowski i in., 2021). Wyjaśnieniem powyższego wyniku może być nakładanie się okresu wysokiej śmiertelności z wylęgiem młodych roztoczy. Takie wytłumaczenie można oprzeć o wyniki Kaczmarka i in. (2011), którzy wykazali, że w podobnych warunkach klimatycznych występują dwa piki zagęszczenia roztoczy z rzędu Mesostigmata - w styczniu oraz na przełomie wiosny i lata.

Niniejsze wyniki wskazują, że na tle innych gatunków drzew, drzewostany sosnowe zapewniają faunie glebowej zarówno najkorzystniejsze warunki bytowe jesienią, jak i najmniej korzystne latem. Efekt ten można wytłumaczyć największą możliwością pochłaniania wody przez ściółkę sosnową jesienią, z największymi spadkami wilgotności w miesiącach suchych (Zhou i in., 2018). Również w drzewostanie brzozowym zagęszczenie, bogactwo gatunkowe i różnorodność roztoczy były istotnie niższe latem niż w drzewostanie sosnowym jesienią. Być może drzewostany brzozowe są mniej zdolne do ochrony wierzchniej warstwy gleby latem przed nagrzewaniem i wysychaniem (Jonczak i in., 2020). Co ciekawe, Ilek i in. (2024) wykazali, że ściółka leśna o niskim stosunku C:N i przeważającym udziale liści dębu, osiągnęła największą zdolność magazynowania wody, podczas gdy ściółka o wysokim stosunku C:N i przeważającym udziale igieł sosnowych miała najniższą zdolność jej magazynowania.

6. Wnioski

Biorąc pod uwagę kluczową rolę fauny glebowej w przebiegu procesów glebotwórczych i dekompozycji, a więc także w przebiegu rekultywacji gleb przekształconych i zdegradowanych, nasza wiedza wymaga dalszego pogłębiania. W tym celu warto kontynuować badania nad poszczególnymi glebowymi ogniwami troficznymi, mającymi swój udział w rozkładzie martwej materii i obiegu pierwiastków w glebie. Wiedza ta jest szczególnie uboga w kontekście złożoności zjawiska, jakim jest wtórna sukcesja leśna na gruntach porolnych. Dzięki wynikom, uzyskanym w ramach przeprowadzonych doświadczeń, można wyciągnąć następujące wnioski:

1. Zgrupowania roztoczy glebowych z rzędu Mesostigmata, zasiedlające grunty porolne, są uboższe pod względem zagęszczenia, bogactwa gatunkowego i różnorodności od tych obecnych na gruntach leśnych. Co więcej, wpływ poszczególnych gatunków drzew na zgrupowania roztoczy również jest zależny od historii użytkowania terenu, dlatego w procesie rekultywacji gleb porolnych istotny staje się odpowiedni dobór składu gatunkowego drzewostanów.
2. Młodsze drzewostany kształtują mniej korzystne warunki do bytowania i rozwoju badanej fauny glebowej w porównaniu z drzewostanami starszymi rosnącymi na gruntach porolnych. Należy zatem prowadzić działania wspierające procesy rekultywacyjne i glebotwórcze w drzewostanowych młodszych klas wieku, między innymi poprzez wprowadzanie gatunków domieszkowych i biocenotycznych wzbogacających wierzchnią warstwę gleby w mikro- i makroelementy w późniejszym etapie funkcjonowania układów siedliskowo-drzewostanowych.
3. W zależności od zmian wilgotnościowych, związanych z cyklem rocznym w klimacie umiarkowanym, drzewostany iglaste generują większe fluktuacje w warunkach mikrosiedliskowych wierzchniej warstwy gleby, a tym samym w strukturze fauny glebowej w porównaniu z drzewostanami liściastymi rosnącymi na gruntach porolnych. Tym samym należy dążyć do zwiększania zróżnicowania gatunkowego drzewostanów już rosnących na tego typu obszarach, jak również uwzględnić większą liczbę gatunków drzew w projektowanych nasadzeniach na gruntach porolnych w przyszłych zalesieniach.

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Spis rycin i tabel

Rycina 1. Poglądowe porównanie profili glebowych na gruncie leśnym (A) i gruncie porolnym z widoczną warstwą płużną, oznaczoną białym wskaźnikiem (B) (Fot. K. Turczański).

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Rycina 5. Aparat Berlesego-Tullgrena w trakcie wypłaszania fauny glebowej (fot. J.Malica).

Rycina 6. Obraz mikroskopowy: (A) osobnika żeńskiego z gatunku *Veiagia nemorensis* oraz (B) osobnika męskiego z gatunku *Oodinychus ovalis* (C.L.Koch, 1839) (fot. J. Malica).

Tabela 1. Podstawowe informacje o układach doświadczalnych.

Tabela 2. Główne wyniki doświadczeń przeprowadzonych w ramach rozprawy doktorskiej.

Tabela 3. Lista wykazanych taksonów roztoczy z rzędu Mesostigmata, w doświadczeniach wykonanych w ramach niniejszej rozprawy doktorskiej. Obecność osobników danego gatunku oznaczono za pomocą symbolu +.

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Review

Soil Environment and Fauna Communities in Europe after Afforestation of Post-Agricultural Lands—A Review

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Abstract: Afforestation can make an important contribution mitigating the effects of changing climate and provide structural and functional benefits. Afforestation also provides challenges for forest managers connected with past land-use history; therefore, there is an urgent need to summarize knowledge about such habitats and point out the gaps in knowledge for planning future studies. Although post-agricultural forests cover a large forest area in Europe, our understanding of the mechanisms governing the below-ground environment is still poor, especially when soil fauna is considered. In this study, we revised knowledge about the soil environment and the response of soil fauna to afforestation on former agricultural lands located in Europe based on research articles from the ISI Web of Science database. Data came from various but distinct locations, compared forests with different types of agricultural lands, and presented previous knowledge about soil chemistry and accompanying soil fauna communities. Finally, we selected 15 studies, investigating soil fauna communities on post-agricultural lands. The meta-analysis was based on response ratio (R) for available data, although in many cases the data were incomplete. Results indicated that post-agricultural forests differ from arable lands in reference to soil pH, but not for soil organic matter and carbon content. Different soil animal groups were represented by a similar number of studies: microfauna (seven studies) and mesofauna (nine), whereas macrofauna were represented by five studies. Meta-analysis revealed that the response of soil fauna to afforestation differed between soil fauna size classes. Additionally, in total, 18 tree species, 12 soil types, and 20 soil parameters were provided in the literature but only a few of them were presented in a single study. Future studies should include the impact of microclimate, detailed stand characteristics and soil conditions, which could help to clearly describe the impact of certain tree species growing on certain soil types. In future soil fauna ecological studies, the data should include mean values, standard deviation (SD) and/or standard effort of means (SE) for abundance, species richness, diversity indices and number of collected samples. Providing the above mentioned information will give the broad audience the opportunity to include data in future comparative analyses.

Keywords: afforestation; edaphon; soil chemistry; soil biodiversity; land use; tree species

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1. Introduction

Forest ecosystems make an important contribution to the global carbon budget, and the significance of forests in the mitigation of climate change has recently gained much attention, not only in science but also in policy discussions [1]. Currently, yearly global deforestation, which especially occurs in tropical zones, is compensated by the formation of forest ecosystems in non-tropical zones on a large scale, such as those located in Europe [2].

Afforestation (formation of forests), as one of the forest management strategies [3], can make an important contribution to mitigating the effects of climate change [4], and provides many structural and functional benefits, including increasing biological diversity, protecting against soil erosion, regulating the hydrologic cycle, and nutrient cycling [5,6].

Contrary to secondary succession, which is a long and complicated natural process returning forests to post-agricultural lands, afforestation is an attempt to speed up this process by planting trees [7]. The afforestation of post-agricultural lands differs from the afforestation of forest habitats and in the results, from simplified species and age composition to specific soil and site conditions of farmlands. Forests established on post-agricultural lands are much more like 'agrocenosis' with changed soil organic matter dynamic and C:N:P stoichometry, and are often accompanied by acidification [8,9]. Therefore, the first generation of forests on post-agricultural land present certain phases of artificially initiated forest establishment processes. Further, afforestation of post-agricultural lands often imposes the growth of a species distinct from the current conditions of that biological community, which can also result in the presence of forest stand diseases [9]. These environmental differences on post-agricultural lands could be related to changes in soil fauna community structure.

Afforestation also provides challenges for forest managers connected with past land-use history. Cultivation (tillage) which aims to turn the soil into a fine tilth to provide the ideal environment for seeds to germinate may also result in a reduction in soil organic matter, physical degradation and erosion [10]. Therefore, arable soils in the initial phase of plant succession differ from forest soils and are characterized by specific chemical and water–air conditions. The difference is caused by fertilization and plowing repeated for many years, resulting in the so-called plow layer, i.e., a compacted layer of soil between the arable and sub-arable layers. This layer retains water and air, which causes the soil to dry out, and these changes may significantly affect the development of soil fauna [11]. These changes in soils may be also reflected in the spreading of pathogens and the occurrence of insect outbreaks in forests, and the lower quality of the wood [12,13].

Although the formation of forests on lands with an agricultural history can provide solutions for the conservation of biological diversity, the mitigation of and adaptation to climate change, and multiple ecosystem goods and services [14], the impact of land-use changes, including afforestation, on terrestrial ecosystems is widespread and well documented; our understanding of the mechanisms governing the below-ground environment is still poor, especially when soil fauna is considered. Additionally, due to the preparation of the UN Decade of Ecosystem Restoration (2021–2030), it is timely to consider where and how naturally regenerating forests and artificially planted forests on land previously used for crops or grazing can contribute to massively up-scaling efforts to restore degraded and lost ecosystems to conserve biological diversity, combat climate change, enhance food security, and protect water supplies in a social, economic, and ecologically effective manner [15].

We focused on the soil environment as it is one of the main global reservoirs of biological diversity [16]. This has a specific hierarchical structure of soil biological diversity which relates to available free space, soil animal body size fractionation, and ecosystem function that create habitats for soil biological diversity across spatial scales [17]. This in turn improves soil aggregation, which enhances soil porosity, water-holding capacity [18] and soil carbon cycling, mediates mineral nutrition of plants in both natural and anthropogenic ecosystems and constitutes soil structure formation and biological regulation [19]. Therefore, comprehensive recognition of their biological diversity may expand our knowledge of ecological mechanisms in former agricultural habitats.

In this study, we revised the knowledge about the soil environment and the response of soil fauna to afforestation on former agricultural lands located in Europe. We focused on European forests as (1) they have similar post-glacial history, and (2) historically, large parts of present-day Europe had been cleared for agriculture and subsequently reforested [20]. We summarized available information regarding where soil fauna was investigated in forests introduced on agricultural landscapes and explored the conditions that influence their abundance, species richness, and diversity. Moreover, we described the impact of the above-ground environment (trees and herb species) on soil characteristics on former agricultural lands. Finally, we examined specific cases where typical temperate tree species were planted on former agricultural lands and how the environment they create affects soil fauna communities.

Our review draws attention to the biological diversity and direction of changes in soil ecosystems in the context of soil chemical composition, dominant tree species and soil animal groups in the temperate forests of Europe. Given the global urgency and ambition for large-scale forest restoration, resulting in mitigation of the climate crisis, our synthesis provides a starting point for complex ecological studies on former agricultural lands and for understanding ecological (positive and negative) consequences on such transformed habitats in ways which promote long-term ecosystem recovery. We hypothesized that afforestation of post-agricultural lands (1) affects soil chemistry, and (2) leads to changes in soil fauna community structure and, regardless, to tree species and location across temperate European forests.

2. Data Collection, Selection Criteria and Meta-Analysis

2.1. Search Methods

The literature reviewed consisted primarily of results from an ISI Web of Science (Clarivate Analytics) database (http://www.isiwebofknowledge.com, accessed on 10 May 2022) search using a combination of the following search strings: post-agricultural land, abandoned fields, forest succession, secondary succession, and soil fauna for the period between 1975 and 2021. Supplementary articles were included from the bibliographic lists of these articles and the previous literature searches conducted by the authors. Articles were only included in the review if they focused on forests in the temperate zone and met the following criteria:

1. The article must be published, peer-reviewed and written in English.
2. The article must have provided documentation of fauna occurrence, abundance, diversity, or other estimates of occupancy in regrowth forest habitat.
3. The article must have made a clear distinction between fauna response to regrowth forests and mature forests or cleared and arable land.
4. The article must have explicitly identified prior cropping or grazing land use for at least one category of regrowth forest.

We did not examine diploma and PhD theses, because we are not aware of any international database that includes them: libraries and databases of some countries include these works, while others do not. We decided to omit them entirely from the search in order to avoid bias.

After excluding studies that did not meet the aforementioned criteria, 15 studies were reviewed. The review first discusses the research on the soil of forests growing on post-agricultural lands, focusing on differences in chemistry and physical structure. Next, the discussion concerns the mutual relation between post-agricultural lands and planted tree species. That part is the introduction to a discussion about the secondary succession of herbaceous plants on abandoned fields as the effect of soil conditions, stand forms and tree species. Finally, the discussion focuses on soil fauna occurrence (including size classes), abundance, and diversity response to regrowth forests on post-agricultural lands, showing the consequence of all the ecological disturbances based on differences in assemblages of organisms on the higher trophic levels.

2.2. Data Grouping and Data Analysis

Due to the low number of articles related to soil fauna on arable lands and post-agricultural forest, we presented the collected data in detail to show the current gaps in knowledge. Additionally, based on the available data, we analysed the effect of afforestation of fields on soil fauna abundance. Meta-analysis effect size was presented as the natural logarithm of the response ratio (lnR). This effect size is most often used when the effects being compared both have positive signs or both have negative signs. The response ratio in this study indicated the average index (Xt and Xc), where Xt is the mean value of index (abundance, richness or Shannon diversity in our case) recorded from post-agricultural forest, and Xc is the mean value of the index on arable habitat.

$$\mathrm{lnR} = \ln \frac{\mathrm{Xt}}{\mathrm{Xc}} = \mathrm{lnXt} - \ln \mathrm{Xc} \tag{1}$$

The effect size of each data pair was obtained by meta-analysis, and the weighted mean effect size, lnR_{++}, and its 95% confidence intervals were obtained by calculating the weight based on the standard deviation. Further, we tested the effect size using meta-regression models with continuous or categorical variables using algorithms in R (www.r-project.org, accessed on 10 May 2022), applying the R studio interface. We used the *metafor* package to aggregate many individual effect sizes into one summary effect size and obtained results on plots using the *ggplot2* package. We considered models significant when $p < 0.05$.

3. Habitat Characteristics

3.1. Location and Types of Examined Habitats

Studies concerning soil fauna communities on post-agricultural lands are generally scarce. The data came from 13 countries, i.e., Belgium [21], Czechia [22], Denmark [23], France [24,25], the United Kingdom [26], Germany [27,28], Hungary [5], Iceland [29], Ireland [30], Poland [31], Slovakia [32], Sweden [33] and Switzerland [34]. Although the study sites represent various locations, drawing a general conclusion about the impact of post-agricultural sites on soil fauna from these locations is almost impossible, as the studies, besides their distant locations, also include different habitat types. For instance, the studies cover the impact of nine habitat types, such as cultivated fields [5,22], abandoned agricultural areas [5,23,25–28,30–32,34], meadows [22], heathlands [29], shrubs [22], forests [5,21–25,27–34], forest plantations [5,29,31] and sand dunes [31], as well as boglands [30]. Data analysis revealed that forests were the most frequently examined habitat. Additionally, the number of habitats included in a single study varied from one habitat, such as forests [21,33] or agricultural areas [26] to five habitats [31]. In some studies, forests were compared with cultivated areas, meadows, and shrubs [22], or with forest plantations [5,29], heatlands [29], and boglands [30].

Data analysis indicated that although forests were the most frequently studied habitat, they were compared with agricultural areas (abandoned, cultivated and meadows). Data analysis revealed that there is a lack of studies which compare forests growing on forest soils (at least in the second generation) with forests introduced on post-agricultural sites with known land-use history. This kind of research could help to understand the dynamic and the direction of soil processes, and also the recovery potential of post-agricultural lands. Moreover, future studies should include various types of habitats located in similar climatic conditions.

3.2. Forest Types on Post-Agricultural Lands

Studies concerning soil fauna in the context of post-agricultural lands include 18 tree species, but for two locations (Ireland and Switzerland), precise data were not provided and the study sites were generally described as ‘forests’. The spectrum of described tree species was dominated by broadleaved species (14 species in total). Among them, European beech (*Fagus sylvatica* L.) was the most frequently reported species, followed by *English oak* (*Quercus robur* L.) and *sessile oak* (*Quercus petraea* (Matt.) Liebl.). Less-studied species were represented by European white *birch* (*Betula pubescens* Ehrh.) and European hornbeam (*Carpinus betulus* L.). On the other hand, coniferous tree species on post-agricultural sites were represented by four taxa, i.e., Siberian larch (*Larix sibirica* Ledeb.), *Sitka spruce* (Picea sitchensis (Bong.) Carrière), *lodgepole pine* (*Pinus contorta* Douglas ex Loudon) and Scots pine (*Pinus sylvestris* L.), *which represent both pure and mixed forests* [19,20,28,30]. Additionally, mixed forests represent various plant communities, such as bog alder forest (*Ribeso nigri-Alnetum*) and fresh coniferous forest (*Querco roboris-Pinetum*) [31]. The number of tree species included in a single study also differs. For instance, five studies included only single tree species, i.e., *Fagus sylvatica* [23,28,33], *Quercus ilex* [25], *Quercus robur* [22], and few studies report three or more tree species [5,26,27,29,32]. However, direct comparison of the published data is difficult, and it is hard to draw any pattern as analyzed forests represent mainly mixed stands with various tree species, different age classes and distinct locations. For instance, Háněl et al. [22] compared 60–80 y/o sub-climax and 100–120 y/o climax oak forests (*Quercus robur*), never used for agriculture, with cultivated and abandoned fields. On the other hand, Nielsen and Nielsen [23] compared 105 y/o pure beech (*Fagus sylvatica* L.) with neighboring arable fields, whereas de la Peña et al. [21] compared mixed young (>30 y/o) forests with ancient forests (>220 y/o) which were composed of the same tree species (*Populus* × *canadensis, Fraxinus excelsior, Acer campestre*, and *Alnus glutinosa*). Moreover, some of the study descriptions do not provide the age of the forests [33]. Additionally, another study presents age differences between experimental (plantations) and control forests. For instance, Harta et al. [5] compared 20 y/o black locust (*Robinia pseudoacacia*) and sessile oak (*Quercus petraea*) plantations with 38 y/o control forests and old-growth forests (*Aceri campestris-Quercetumpetraeae-roboris*). Therefore, studies that include various tree species of the same age, or the same tree species in different age classes, may help to understand the impact of afforestation on the soil environment. The spectrum of the species introduced on post-agricultural lands is wide, which is in line with the afforestation policy. It is recommended that many tree species are planted, with a high range of broadleaved species, which are considered to be more resistant to various environmental agents. They also support the creation of forest habitats by soil biota and enhancing soil processes [13].

Published studies indicated that tree species by the land-use type affected soil chemistry, understory vegetation, above-ground invertebrate community, and nutrients in plants. For instance, de la Peña et al. [21] reported higher phosphorous content and lower potassium values in forests on post-agricultural sites when compared to 220 y/o ancient forests composed of *Populus* × *canadensis, Fraxinus excelsior, Acer campestre* and *Alnus glutinosa*. Additionally, these sites did not differ in terms of the total nitrogen in the soil environment. The cited studies also indicated that post-agricultural forests were characterized by higher phosphorus concentration in plants whereas the plant biomass did not differ between the forest. The comparison of old-growth relict forest (*Aceri campestris-Quercetum petraeae-roboris*) with black locust (*Robinia pseudoacacia*) and sessile oak (*Quercus petraea*) plantations indicated that old-growth relict forests were characterized by the highest soil plasticity and the highest soil organic matter. Moreover, sessile oak plantations were characterized by low pH values, whereas this parameter was similar between black locust plantations and both arable fields and managed-control black locust forests [5]. Therefore, there is a need to include in future studies many tree species, both broadleaved and coniferous, which are the most popular tree in European forests. Such studies could help to understand and predict recovery scenarios in post-agricultural habitats. Additionally, studies which include forests from various age classes may provide information on the recovery dynamic in above- and below-ground environments.

4. Effect of Afforestation on Soil Chemistry

The soils on post-agricultural lands in the initial phase of plant succession differ from forest soils and are characterized by specific chemical and water–air conditions. The difference is caused by the so-called plow layer, which retains water and air, and thus causes the soil to dry out; these changes may significantly affect the development of soil fauna [11]. The spectrum of the soils reported from post-agricultural lands is generally wide. The articles reported that soil fauna in these habitats was investigated in a total of 12 soil types. The soils included acrisols [24], andosols [29], cambisols [22,27,30,32,33], chernozems [32], gleysols [27,30], histosols and leptosols [30], as well as luvisols [25], phaeozems [5], podzols [23,30] and stagnozols [32]. The analysis indicated that cambisols were the most frequently reported and were included in four studies, followed by podzols, noted in two articles. Interestingly, various tree species were reported from the same soil type. For instance, cambisols were covered by 13 tree species, and stagnosols and chernozems by 9 tree species. Some most common soils, such as podzols, were covered by one species, i.e., European beech, whilst there were no data on rusty soils which dominated in some European countries. Therefore, it seems to be important to plan in future studies for other soil types covered with the same tree species in a single study.

Soils between post-agricultural lands and forests differ when soil physical and chemical compounds are analyzed. Published data included the analysis of soil structure [35], soil moisture [24,32], water content [28], soil pH [5,21,22,24,32,34,36,37], phosphorus (P) [5,21,25,29], nitrogen (N) [5,25,28,32,36], carbon (C) [5,25,28,32,36], aluminum (Al), calcium (Ca), magnesium (Mg) and potassium (K) [5,21] (Figure 1d). Data analysis indicated that soil acidity, nitrogen, carbon and potassium content were frequently reported from post-agricultural habitats (Table 1).

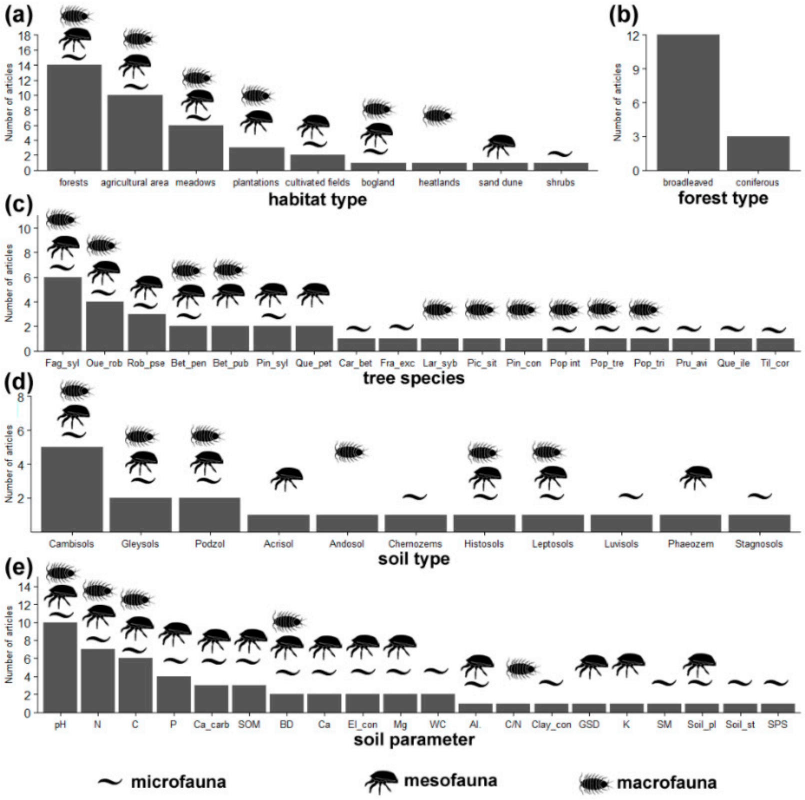

Figure 1. Habitat types (**a**), forest types (**b**), tree species (**c**), soil types (**d**) and soil parameters (**e**) reported from publications on post-agricultural sites. Tree species abbreviations are based on the first three letters of the genus and species name of the tree species. Soil parameter abbreviations indicate: pH—acidity, N—Nitrogen, C—Carbon, P—Phosphorus, Ca_carb—calcium carbonate, SOM—soil organic matter, BD—bulk density, Ca—calcium, El_con—electric conductivity, Mg—Magnesium, WC—water content, Al—Aluminum, C/N—carbon-to-nitrogen ratio, Clay_con—clay content, GSD—grain size distribution, K—Potassium, SM—soil moisture, Soil_pl—soil plasticity, Soil_st—soil structure, SPS—soil particle size.

Table 1. Summary of the studies investigating the communities of soil fauna on post-agricultural lands. Abbreviations indicate: SM—soil moisture, SOM—soil organic matter. Age class of forests were applied as follows: 1–30 young forest, 31–80 middle age forest, 81 > mature forest. Summary based on [5,22–34,36].

Groups of Organisms	Experimental Type	Agriculture Activities	Period of Sampling	Forest Type and Age Class of Stands	Analyzed Physical Parameters	Location	Authors
Macrofauna	Secondary succession studies	treated with weed-killer, shallow ploughed, harrowed, lightly rolled	~1.5 year	Forest type: broadleaved Age class: middle aged forest	-	United Kingdom	Southwood et al. [26]
Macrofauna	Energetic plants species studies	Arable field	4 years	Forest type: broadleaved Age class: young forest	pH, Carbon, NO_3	Germany	Makeschin [27]
Mesofauna and macrofauna	Secondary succession studies	Arable field, sown with grain	1 year	Forest type: broadleaved Age class: middle aged and mature forest	Carbon, Nitrogen, Soil Bulk Density	Germany	Scheu and Schulz [28]
Mesofauna	Secondary succession studies	Fields fertilized, harrowed, ploughed and cultivated	1 year	Forest type: broadleaved Age class: no data	pH	Sweden, Netherlands, Spain	Gormsen et al. [33]
Macrofauna	Secondary succession studies	Arable filed, treated with pesticides, ploughed, cropped with winter barley	7 years	Forest type: broadleaved Age class: mature forest	pH	Denmark	Nielsen and Nielsen [23]
Microfauna	Secondary succession studies	Abandoned arable field	12 years	Forest type: broadleaved Age class: middle aged and mature forest	pH SOC	Czech Republic	Háněl [22]
Microfauna, Mesofauna, Macrofauna	Impact of land use type	-	-	-	-	Ireland	Keith et al. [30]
Macrofauna	Impact of afforestation	Sheep grazing	2 years	Forest type: coniferous and broadleaved Age class: young and middle aged forest	pH, Carbon, Nitrogen, C/N	Iceland	Sigurdsson and Gudleifsson [29]
Macrofauna	-	-	6 years	-	-	Poland	Szczepko et al. [31]
Mesofauna	Impact of soil	Pastures	1 year	Forest type: broadleaved Age class: mature forest	pH	France	Heiniger et al. [24]
Mesofauna	Secondary succession studies	Wheat field, grassland	2 years	-	-	Switzerland	Jaffuel et al. [34]
Macrofauna	Impact of afforestation	Arable field cropped with winter wheat	1 year	Forest type: broadleaved Age class: young forest	pH, Carbon, Nitrogen, Bulk density	UK	Briones et al. [36]
Microfauna	Secondary succession studies	Arable field, pastures	1 year	Forest type: broadleaved Age class: no data	pH, Carbon, Nitrogen, C/N	France	Jackson et al. [25]
Mesofauna	Impact of afforestation	Arable field, abandoned field	1 year	Forest type: broadleaved Age class: young and mature forest	pH, SOM, Ca, Mg, N, $CaCO_3$	Hungary	Harta et al. [5]
Microfauna	Secondary succession studies	Arable field, Meadow	1 year	Forest type: broadleaved Age class: no data	pH, Carbon. Nitrogen, Sulphur, C/N, SM	Slovakia	Renčo et al. [32]

Analysis of available data indicated that soil acidity was higher on agricultural lands (6.14 ± 0.32) than in forests (4.94 ± 0.39), and that the difference was significantly different ($p < 0.01$). Additionally, soil organic matter was lower on agricultural lands (1.35 ± 0.73) than in forests (5.56 ± 2.27) but did not differ significantly ($p > 0.05$). Further, our data analysis revealed that agricultural lands had lower carbon content (2.73 ± 1.09) than in forests (9.20 ± 6.79), but the difference was insignificant ($p > 0.05$) (Figure 2).

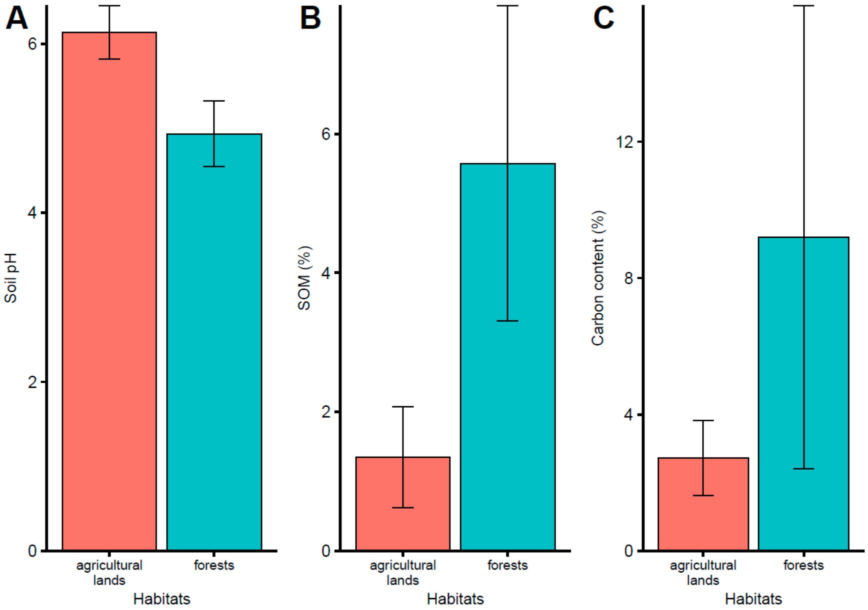

Figure 2. Soil pH (**A**), soil organic matter (**B**), and carbon content (**C**) reported from agricultural areas and from post-agricultural forests based on literature survey. Bar plots represent mean values, whereas whiskers represent standard deviation (SD).

4.1. Soil Acidification

Soil acidification, normally indicated by the pH decline of a certain soil, is a slow natural process that occurs during pedogenesis, which can be accelerated or slowed down by farming practices [38]. On post-agricultural lands, soil acidification is a result of long-term liming, which enhances crop production [39]. The majority of the published data proved that soil pH was generally higher on former agricultural lands [22,24,29,32,34], although some research reported similar pH values [5,25,36] or even lower pH [21] when compared to forest habitats. Detailed analysis indicated that in some cases the tendency differed. For instance, higher pH values were noticed in forests when they were compared with (1) both meadows and agricultural fields [32,34], (2) both cultivated and abandoned fields [22], (3) open heatlands [29] and (4) pasture [24]. Interestingly, similar pH values were found in agricultural fields, forests and border zones between these habitats [25], between arable fields an willow plantations [36] and also between forests, reforested sites and intensively managed agricultural areas [5]. Only a single study reported lower pH values from post-agricultural forests when compared to ancient forests (4.48 vs. 5.36) [21].

4.2. Nitrogen Content

Nitrogen is a fundamental component of living organisms which occur in two large nitrogen pools on Earth [40,41]. Data on the total nitrogen content of post-agricultural lands are ambiguous, and it is difficult to define any pattern. For instance, total nitrogen content did not differ between forests and pasture [24], or was similar but significantly different between arable fields and willow coppice [36]. Further, some studies indicated that nitrogen content was higher in agricultural fields. For instance, two-times-higher nitrogen content was reported in arable lands than in forests [25]. On the other hand, some studies presented two-times-higher nitrogen values from forests and meadows than from agricultural fields [32]. Similarly, Harta et al. [5] recorded six-times-higher nitrogen (NO_3) content in relict forests than in reforested sites or abandoned fields, compared to two-times-higher nitrogen (NH_4^-) content on afforested sites than in forests or abandoned fields (both cultivated or abandoned). Additionally, two-times-higher nitrogen values were noticed from forests compared to abandoned fields, and the values were higher in the top 0–3 cm layers than from 3–6 cm [28]. The nitrogen content may also differ between heathlands and birch woodlands and spruce or pine plantations, but the trends differed between Eastern and Western locations [29]. Total nitrogen content did not differ between ancient forests and post-agricultural forests (2989 vs. 3065 ppm) [21].

4.3. Phosphorous Content

Phosphorus (P) is an essential nutrient element for life, and its transformation during ecosystem development exerts a crucial influence on soil fertility and ecosystem properties [42]. Research on post-agricultural lands which include data on phosphorous are limited. Analysis of total and bioavailable phosphorous content in published articles indicated that the content was generally higher in post-agricultural land compared to forest sites [5,21,25]. Total phosphorus content was at least two times higher (987 vs. 479 ppm) [21], whereas bioavailable phosphorous content was two [5,25] to seven times higher on post-agricultural lands (67.57 vs. 9.0) [21].

4.4. Carbon Content

Soil is the largest reservoir of carbon, which exceeds the amount of carbon in the atmosphere and terrestrial vegetation. Published data revealed that carbon content was generally 2× higher in forests than in cultivated or abandoned (for 11 years) post-agricultural land, and the differences were more pronounced in the top 0–3 cm layers than in lower layers [28]. Carbon concentration reached 5.2%–6.4% on heatlands, 7.5%–12.9% on birch woodlands, 5.1%–6.9% on larch plantations, 8.2%–11.6% on pine plantations and 10.1%–16.3% on spruce plantations in Iceland [29]. Total carbon content was 3.5× higher in the forests than the arable fields in a Mediterranean landscape [25]. On the other hand, carbon content did not differ between arable fields and willow coppice, and varied from 1.56% to 1.80% [36]. Moreover, organic carbon content was two times higher in meadows and forests than in agricultural fields [32].

4.5. Aluminum, Calcium, Potassium, and Magnesium Concentration

Aluminum, calcium, potassium, and magnesium concentrations were generally scarcely studied on post-agricultural lands. Aluminum (65.2 vs. 69.7 ppm) and magnesium (194.9 vs. 190.4 ppm) concentration did not differ between ancient forests and post-agricultural land, but potassium (163.0 vs. 113.2 ppm) and calcium (2946 vs. 2353 ppm) concentrations were significantly lower on post-agricultural land [21]. Available potassium concentration was lower in sessile forests and black locust forests in comparison to cultivated agricultural land and managed oak forests [5]. Additionally, higher calcium concentrations were noticed in abandoned agricultural fields [5].

4.6. Carbon to Nitrogen Ratio and Nitrogen to Phosphorous Ratio

The information on the C-to-N ratio on former agricultural lands were represented by few studies. The ratio was ca. 50% higher in forests than on former agricultural land (15.2 vs. 10.3) [25]. On the other hand, the C-to-N ratio did not differ according to land use (14.6 vs. 14.8) [21]. Although the precise values of the ratio were sometimes not provided, the stechiometry affected soil fauna abundance, richness and diversity [29]. The N-to-P ratio was scarcely reported in studies when soil fauna was concerned. The N-to-P ratio was clearly different in post-agricultural soils, with the values being half those found in ancient soils (7.0 vs. 3.1) [21].

4.7. Soil Moisture

Water availability is a major determinant of soil animal community composition and functioning. Below-ground ecosystems are affected by soil moisture controls on several aspects of soil chemistry, including nutrient availability and leaching rates, and moisture availability (along with temperature) is an important driver of decomposition rates globally [43]. Soil moisture was higher in forests than in pasture soils [24]. Water content was positively correlated with the organic matter content in soils and was inversely related to soil bulk density, which was the lowest in beech forests [28]. Soil moisture differed between land use types and ranged from ~22% in agricultural fields to ~31% in forests [32].

Although published research concerning soil fauna studies includes various habitat types (Figure 1a), they are generally based on contrasts between cultivated or abandoned fields undergoing succession processes and forests. However, there is little knowledge on how growing forests affect soil environment, i.e., soil structure and physical or chemical characteristics, especially when time is concerned. Analysis of the published data indicate that some parameters, such as soil acidity, carbon and nitrogen content, are more frequently reported than other soil parameters (Figure 1e).

5. Effect of Afforestation on Soil Fauna

5.1. Soil Fauna Classes

Soil biota plays an essential role in ecosystem functioning, especially in biogeochemical cycles with feedback on plant diversity, abundance, succession and productivity [44]. Soil fungi and bacteria break down organic matter using an arsenal of hydrolytic and lignolytic enzymes that provide available nutrients for plants and other soil organisms, whereas microfauna (<100 µm diameter), mesofauna (100 µm to 2 mm diameter) and macrofauna (>2 mm diameter) [45] enhance nutrient cycling through plant litter and organic matter comminution and by grazing microbial biomass [46]. For instance, microfauna were included in seven studies [21,22,25,27,30,32,34] and mesofauna were reported in nine studies [5,21,23,24,26,28,30,31,33], whereas macrofauna were noted in five studies [26–30]. However, most of the studies included soil fauna from certain size classes. The literature survey also indicated that forests, agricultural areas and meadows were the most frequently studied habitats, including three soil fauna classes, and that five soil types (cambisols, gleysols, histosols, leptosols and podzols) include three soil fauna classes (Figure 2A,B). Animals from all three groups were included in a single study [30], but the study did not provide tree species. Therefore, for better understanding the response of soil fauna to changes during recovery of the plant communities on post-agricultural sites, it is crucial to conduct a comprehensive study which includes various animal groups.

Our meta-analysis indicated that the response of soil fauna on farmlands to afforestation differed between soil fauna classes. A negative response ratio was recorded for diptera (-1.46) and no response was noted for nematodes (-0.18), whereas a positive response was seen for nematodes (0.63) and collembolas (2.17) (Figure 3).

5.2. Soil Microfauna

Our analysis indicated that microfauna in post-agricultural studies were represented by soil microbes [21,27,30,32] and nematodes, which were analyzed with tardigrades [21,22,25,30,32,34]. Microfauna was reported from eight soil types, i.e., cambisols, chernozem, gleysols, histosols, leptosols, luvisols, podzols, and stagnozols, which were covered in total by 13 tree species (Figure 1c). Renčo at al. [32] studied soil nematode communities and microbial diversity and the properties of three soil types (stagnosols, cambisols, chernozems) in forest, meadow, and agriculture habitats of the Slovak Republic. They proved that species richness and diversity were highest in the forest soils on chernozem, while the lowest in the agriculture soils on stagnosol. The forest soil also had the highest nematode abundance within functional guilds and microbial richness and diversity. The abundance of most nematode guilds, nematode species richness and microbial richness tended to be higher in soils with higher pH, N and C contents. They also proved that sampling dates had minimal importance for most of the studied parameters. On the other hand, Keith at al. [30] analyzed the relationships between diversity and nematodes, mites, earthworms and ants across a general gradient of different land uses—arable, pasture, rough-grazing, forest and bogland. For nematodes, the species richness was the highest in pastures, for mites in rough-grazing land and in bogland for ants. Jaffuel at al. [34] compared the communities of entomopathogenic nematodes of agriculture area, forest and grassland. The highest abundance was recorded in the forest ecosystem, and the lowest in the wheat field, whereas the highest abundance of free-living nematodes was recorded in grassland, and, significantly, the lowest in forests. Háněl [22] compared secondary succession of nematodes in 1–48-y/o abandoned fields on cambisols with cultivated fields and sub-climax oak forests. In the cultivated fields, the bacterivores were the predominant group. The abundance of nematodes in the abandoned field was similar to cultivated fields for the first three years of succession. In 7–8-year-old abandoned fields, the abundance was almost five times higher, and the plant parasites were the dominating group. The study showed low total abundance of nematodes in the 12–13-year-old willow shrubs and increase of abundance in the 35–48-year-old birch shrub stage. The nematode assemblages became similar to forest communities.

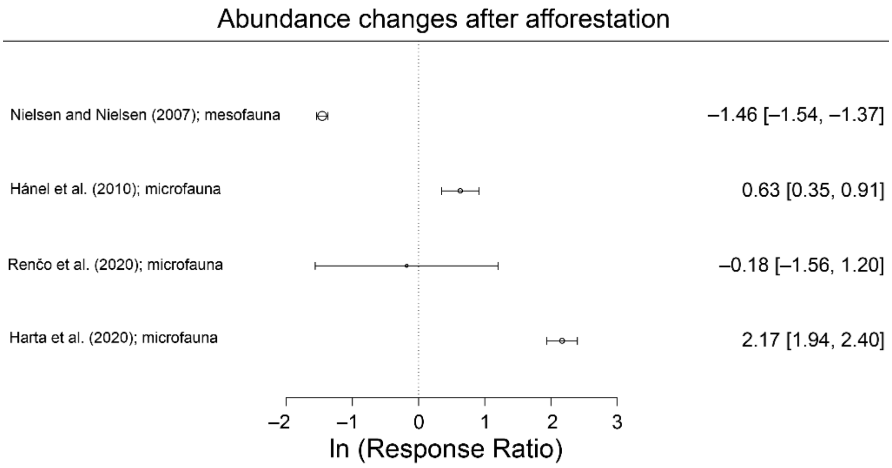

Figure 3. Effect of afforestation of arable lands on soil fauna abundance. The error bars represent 95% confidence intervals (CIs). The circle represents the effect size [5,22,23,32].

Our analysis indicated that microfauna studies include the analysis of 16 soil parameters. In general, among them, soil pH was reported in six articles, followed by carbon and nitrogen content, represented by three studies. Soil pH was lower in broadleaved (pH: 5.4–5.7) than in coniferous forests (pH: 5.7) [22,25,32]. The carbon content was lower in coniferous forests (2.4%) than in broadleaved forests (3%–4%). Similarly, nitrogen content was also lower in coniferous forests (0.2%) than in broadleaved (0.36%–1.3%) [22,25,32]. Further, soil moisture was lower in coniferous forests (24.2%) than in broadleaved forests (26.1%) [32]. Most of the parameters were provided in a single study, such as electric conductivity (Figure 1d), therefore it is difficult to draw summarizing conclusions on them at the habitat, forest or tree species level. Therefore, there is an urgent need to include many soil parameters in future studies, which could allow comparison of the obtained data.

The studies on microfauna differ in the number and type of analyzed ecological indices. Most of the studies were based mainly on abundance, which is presented as total value [21,34], calculated per square meter [22] or per 100 g of soil [25]. For instance, nematode densities reached 1350 × 10^3 per square meter [22] or 1110 ind. per 100 g of soil [25] in broadleaved forests, but there are no data from coniferous forests. Data analyses also present species richness, but only for broadleaved forests [22,25,30,32]. Additionally, data analysis indicated that Shannon diversity was slightly higher in broadleaved (2.97) than in coniferous (2.84) forests [32]. The literature indicated other ecological characteristics, such as basal index, plant parasite index and enrichment index [22,25,32], or functional guilds [32], though the number of analyzed ecological parameters was large.

5.3. Soil Mesofauna

Studies concerning soil mesofauna included mites [28,30,33], springtails [5,24,30], dipteran [23], Hymenoptera [26,31] and ants (Formicidae) [30]. A single study reported soil fauna as an invertebrate community [21]. These animal groups were noticed from eight soil types, i.e., acrisol [24], cambisols [30,33], gleysols, histosols, leptosols [30], phaeozem [5], and podzol [23,30]. The reported studies include seven tree species. Scheu and Schulz [28] proved that along with changes in plant species and soil formation, there were also changes in the species composition and diversity of moss mites (Oribatida). Additionally, the accumulation of soil carbon was accompanied by the development of the species-rich community of moss mites (Oribatida). In the early succession stages, moss mites mostly colonized the litter layer, while most mites inhabited the upper mineral layer. Moreover, de la Peña et al. [21] compared both plant communities and herbivores of stands on post-agricultural and forest land. Their results indicated an increased number of herbivorous microorganisms because of a higher phosphorus content in plants found on post-agricultural land. Thus, it has been suggested that this relationship may be responsible for the difficulties in the reconstruction of the forest environment in agricultural areas. Harta et al. [5] examined springtail communities of two 20-year-old plantations of black locust and sessile oak that had undergone long-term fertilization experiments before the afforestation. These authors proved that the highest species richness was observed in the relict oak stand, while the cultivated fields were characterized by the lowest species richness. Additionally, species richness and Shannon diversity of the oak and black locust forest plantations were higher compared to the cultivated fields. Compared to control forest habitats, the diversity of plantations was significantly lower. A more diverse springtail community was described in the oak plantation than in the plantation of black locust. The highest abundance was noticed in the old relict oak forest, while the abundance on plantations was averaged 2.5 times higher than in arable fields. Moreover, studies on dipteran fauna indicated that species richness was higher in beech stands than in arable fields, and the community included many rare species. Interestingly, the increase of mite density was noticed after abandoning agricultural practices, but the species richness was not changed. Mite densities were not affected by sowing plant seeds, but in response to management of plant community, the community composition of mites was changed [33].

Our analysis indicated that mesofauna studies also include the analysis of soil parameters. In general, 14 soil characteristics were reported from these studies, and among them, soil pH and nitrogen were reported in four studies [5,21,24,28,33], followed by phosphorus content, represented by three articles [5,21,33]. Other soil parameters were less frequently reported from post-agricultural habitats (Figure 1d). Soil pH ranged from ca. 5 to 7.3 and increased with afforestation, which may lead to great changes in springtail communities [5,33]. Springtail communities were also shaped by soil plasticity, SOM, phosphorus content and, to a lesser extent, by N-to-P content [5] and by microclimate conditions, which were reported as key drivers [24]. Two studies included soil microarthropods (mites) which represent Astigmata, Mesostigmata, Oribatida, and Prostigmata. The diversity of mite communities did not change after abandoning agriculture, and the proportion of predators (Mesostigmata) was equally represented in all the field sites [28,33].

The studies on mesofauna differ in the number and type of analyzed ecological indices. The analysed articles provide abundance [24,26,30,31], relative abundance [23,24,31], density per square meter [5,33], relative frequency and indicator value [31], species richness [5,23,24,24,26,28,30,31], Sørensen index of similarity [26], Shannon diversity [5,33], Pielou's evenness index and community dominance index [5], canonical correspondence analysis (CCA) [5,28,33], principal component analysis (PCA) [24], redundancy analysis (RDA) [30], and trophic groups [23,33]. The majority of the studies provide abundance and species richness; however, other ecological indices were presented in different numbers of the studies.

5.4. Soil Macrofauna

Studies concerning soil macrofauna include various animal groups such as Carabidae [27], Coleoptera [26], Diplopoda [28], Isopoda [28], Lumbricidae [27–30] and Opiliones [27]. They were reported form six soil types such as andosol [29], cambisols and gleysols [27,30], histosols, podzols and leptosols [30]. Scheu and Schulz [28] revealed that changes in plant communities and in soil formation lead to changes in species composition and diversity of Ribeso nigri-Alnetum (Lumbricidae, Diplopoda, Isopoda). Additionally, published data proved that afforestation (intentional and natural) of open areas and removal of old abandoned wooden buildings may limit land heterogeneity, and thus diversity of insects, in various types of habitats, including post-agricultural areas with bog alder forest (*Ribeso nigri-Alnetum*) and fresh coniferous forest [31]. Southwood et al. [26] proved that an increase of vegetation diversity is mostly correlated with an increase of Coleoptera and Heteroptera diversity in the early stages of secondary succession. Makeschin [27] studied the impact of energy forestry on soil fauna. The results showed that afforestation and fertilization increased abundance, biomass and species richness of Lumbricidae, but decreased abundance of Carabidae and Opilionida [31]. Keith et al. [30] compared Limbricidae and Formicidae communities in five land use types (arable, pasture, forest, rough-grazing, and bogland). They observed that communities of each group in forest and rough-grazing land were similar, but communities of other land types were significantly different [34]. Sigurdsson and Gudleifsson [29] examined the impact of afforestation on Lumbricidae assemblages and proved that they were positively related to N, but not to C/N and pH [33]. Furthermore, Briones et al. [36] revealed that the density and biomass of earthworms were higher in the arable land than in the plantations of Willow or Miscanthus [39]. Nielsen and Nielsen [23] compared Diptera communities of a beech stand and arable field. They reported that species richness of Diptera was higher in the beech stand but abundance and biomass were higher on arable field [27].

Only four macrofauna studies reported more than one soil parameter. Soil pH in the studies of Makeschin [27] ranged from 5.6 to 6.4, carbon from 0.7% to 1.8% and NO_3 from 0 to 40 mg/L [31]. Scheu and Schulz [28] proved that carbon and nitrogen content were higher, but soil bulk density was lower, in the soil of beech stands than in the soil of wheat filed and fallows [32]. Sigurdsson and Gudleifsson [29] revealed that soil pH was higher in the heathlands than in birch, larch and pine stands but the carbon content and C/N ratio were higher in these stands and increased with their age [33]. Briones et al. [36] reported that soil bulk density of Miscanthus and Willow plantations were similar and higher than in arable lands (1.48/1.45/1.25 g/cm^3). Soil pH on willow plantations (6.75) and arable land (6.68) were similar and higher than in the Miscanthus plantation (5.97) [39].

Data analysis indicated that macrofauna communities were characterized by abundance [26,27], density per square meter [29], species richness [26,27,29], Shannon diversity [28,30], biomass [27,29], and canonical correspondence analysis (CCA) [28]. Similarly to mesofauna, macrofauna was characterized mainly by abundance and species richness, but the number of analysed indices was lower.

6. Planning Future Studies in Forest on Post-Agricultural Lands

The conducted literature survey indicated that there is a lack of studies on pure forests with detailed characteristics of stands such as age, tree density (ha^{-1}), canopy closure, tree dimension at breast height (DBH), and with detailed characteristics of the undergrowth species based on the popular Braun–Blanquet scale. Additionally, future studies should include the impact of microclimatic and soil conditions, which could help to clearly describe the impact of certain tree species growing on certain soil types. The analysis of organic matter thickness could provide information on the litter input to the soil environment. Additionally, soil chemistry, which includes several soil parameters, mainly based on soil moisture and the carbon-to-nitrogen and nitrogen-to-phosphorus ratios could fill the gap in the knowledge on post-agricultural forests. The future data analyses should also be based on abundance (m^{-1}), species richness and Shannon diversity (H′), supported by general linear model (GLM) analysis and community analyses (CA, CCA, RDA or PCA). The meta-analysis also revealed that although the number of articles with certain data (soil parameters or soil fauna characteristics) seemed to be sufficient to obtain valuable information (from three to nine per group) based on calculated effect size, the majority of the studies lacked important information. Therefore, in future soil fauna ecological studies, the data should include mean values, standard deviation (SD) and/or standard effort of means (SE) for abundance, species richness, and diversity indices and number of collected samples. Providing the above-mentioned information will give a broad audience the opportunity to include data in future comparative analyses.

7. Conclusions

Research on soil fauna on post-agricultural land has been conducted for many years, but knowledge about the processes taking place in these areas is still insufficient. Some of the published works discuss the succession processes in agricultural areas without the analysis of soil fauna groups. Others, on the other hand, compare extremely different habitats, such as agricultural land and forests. It is difficult to obtain information on the dynamics and pace of processes occurring in the soil environment of forests on post-agricultural lands, and thus in the assemblages of animals inhabiting the soil, from the published works. The first generation of the forest growing in the post-agricultural land very often disappears after several decades due to the changed physicochemical and biological conditions of the soil. The detailed understanding of the mechanisms shaping biological diversity in the soil of such forests can help in a better selection of the species composition of the forest in the initial stage and thus ensure an increase in its stability for many years.

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RESEARCH ARTICLE

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Impact of land use history and soil properties on soil mite communities (Acari, Mesostigmata) inhabiting stands growing on post-agricultural land

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Abstract

Decades of agriculture in a former—type of ecosystem, for example, deciduous forests—result in severe habitat degradation. The planted tree species encounter harsh conditions due to physically and chemically transformed soil environments. In addition, afforestation itself significantly modifies the upper soil horizons. It may impact the soil fauna communities, including mites from the Mesostigmata order (Mesostigmata = Gamasida). Due to their sensitivity, mesostigmatid mites are good bioindicators of changes in the soil. A decrease in the density, species richness, and diversity of mites indicates disturbances in the soil environment and may confirm the impact of agricultural practice on the soil environment. Our research aim was to examine the impact of soil properties and land use history on the mesostigmatid mite communities in stands growing on forest and post-agricultural lands. These sites were afforested with different tree species (*Betula pendula* Roth., *Fagus sylvatica* L., *Pinus sylvestris* L., and *Quercus robur* L.). Thus, 21 research plots were established on forest and post-agricultural land, each on rusty soils considered to be one of the most common in Central European forests. We collected a total of 567 soil samples during three sampling sessions in spring and autumn for soil Mesostigmata investigation. We also described the soil profile on each plot and collected soil and litter samples to measure pH, litter thickness, soil organic matter, bulk density, soil moisture, soil organic carbon, and elements content. Our study revealed that 16 out of 30 environmental parameters differed between habitat types. A total of 1355 mites were classified into 58 taxa (50 species and 8 genera). The most numerous species were *Veigaia nemorensis* (165 ind.; 12.2% of all mesostigmatid mites), *Zercon peltatus* (156; 11.5%), and *Paragamasus conus* (141; 10.4%). The highest abundance was recorded in birch stands on forest land, whereas the lowest abundance for oak stands growing on post-agricultural land. Interestingly, in oak stands we recorded both the highest diversity of mite communities (forest land) and the lowest on post-agricultural land. Furthermore, our study showed that post-agricultural land and Na content in forest litter affected the abundance, species richness, and diversity of mesostigmatid mite communities. Species richness was additionally affected by tree species, that is, pine and oak. Our research indicated that long-term agricultural practice negatively affected the density, species richness, and diversity of Mesostigmata communities 20 years after afforestation.

KEYWORDS

Acari, afforestation, forest biodiversity, forest soils, Mesostigmata, post-agricultural land, soil fauna

1 | INTRODUCTION

Afforestation of post-agricultural land is one of the most challenging undertakings in forestry due to the loss of biological diversity and changes in biological, chemical, and physical properties (De Schrijver et al., 2012; Scheu & Schulz, 1996). Soil properties deformation on post-agricultural land may hamper the growth of root systems and the physiological development of trees (Gorzelak, 1996; Sierota, 2011). The negative impact of agriculture and food production on soils results from (1) deforestation and (2) repeated plowing and fertilization. Deforestation removes plant root systems and leads to the absence of lignin and root secretions. Their presence determines the biodegradation of humus (Gorzelak, 1996; Yang et al., 2021) and maintains a specific micro-environment (Sahani & Behera, 2001) in which soil, soil organisms, and tree root systems interact (Heiniger et al., 2015). On the other hand, repeated plowing is responsible for the final transformation of the soil profile, and repeated fertilization leads to soil chemical modifications (Gorzelak, 1996; Renčo et al., 2020; Rosenzweig et al., 2016). All these effects may shape ecological processes related to soil fauna communities, such as soil fauna abundance, species richness, diversity, and biomass in post-agricultural soils (Briones et al., 2019; Makeschin, 1994; Nielsen & Nielsen, 2007). Habitat transformation from forest into agricultural lands may alter the organic matter cycle and soil trophic relationships (Norton et al., 1993), which increases the risk of spreading pathogens and insect gradations on post-agricultural lands compared to forests (Bernacki, 1990; Sobczak, 1996).

The response of soil fauna communities to environmental changes has been widely described (Chauvat et al., 2003; Erdmann et al., 2006; Zaitsev & van Straalen, 2001) however, only a few studies concern afforestation as an environmental factor in post-agricultural lands (Gormsen et al., 2006; Scheu & Schulz, 1996). Additionally, those studies analyzed the impact of only single tree species and a few soil and litter parameters. Only a few studies in Europe have explored the impact of post-agricultural land afforestation on soil mesofauna communities, including mites (Malica et al., 2022). Therefore, there is an urgent need to explore how the afforestation of post-agricultural lands by widely distributed European tree species affects soil properties and soil mite communities. We used soil mesostigmatid mites (Acari, Mesostigmata = Gamasida) as model organisms due to their key role in the soil food web (Koehler, 1999; Wissuwa et al., 2012). Considering diverse behavioral, trophic, and ecological traits, soil mesostigmatid mite communities are perfect bioindicators (Urbanowski et al., 2021).

Our research aims to analyze the impact of four tree species (*Pinus sylvestris* L., *Betula pendula* Roth., *Quercus robur* L., and *Fagus sylvatica* L.) on soil mesostigmatid assemblages and soil and litter properties (physical and chemical) in young (22 y/o.) stands growing on post-agricultural and forest lands. We hypothesized that (1) post-agricultural rusty soils differ from forest rusty soils in physical and chemical properties, (2) abundance and diversity of Mesostigmatid mite communities change in response to soil properties, and (3) tree species affect soil fauna communities.

2 | MATERIALS AND METHODS

2.1 | Study site and experiment design

The research was conducted in the Opole Forest District (south-western Poland; 50°83′93″ N, 17°44′53″ E). We chose this area because of the large-scale afforestation of agricultural land in the 1990s. All plots were consistent in terms of soil type and geological properties (Figure 1). The forest area selected for the studies includes the Dąbrowa forest complex with a cover of 5479.07 ha. The mean forest age in the forest complex is 59 years. Coniferous forests cover 60% of the forest area, whereas the forest complex consists of Scots pine (86%), oak (5%), birch (4%), and other species. According to the soil moisture, the forests are dominated by fresh forest sites (57% of the area), moist forest sites (40%), and marsh (~3%). Mean annual precipitation is ~603 mm, and the mean annual temperature reaches ~8°C. The vegetation season lasts ~227 days. The soils within the study area are dominated by rusty soils (Arenosols acc. to IUSS Working Group WRB, 2015)—45.3%, which are considered to be the most common in the Forest States in Poland (Rutkowski et al., 2021).

A total of 21 study sites (each plot = 0.02 ha) were established on post-agricultural (Scots pine, silver birch, and oak) and forest land (Scots pine, silver birch, oak, and European beech) (Figure 2). European beech on forest land was studied for a broader comparison of deciduous species. The forests were chosen based on the following criteria: the presence of the same soil type (rusty soil; Arenosol acc. to

IUSS WRB, 2015), habitat type (fresh coniferous forest), and age (22 y/o), while they undergo different land use practice (post-agricultural lands vs. forest lands). The minimal distance between the plots was ∼30 m to avoid pseudoreplication and maintain similarity between microhabitat and soil conditions. The study site characteristics were conducted in June (the climax of the growing season) to note all plant species growing on each study site. On each study site, we determined the total number of trees (N), the height of the trees (m), and the dimension at breast height (cm). All vascular plants were recorded in each vegetation plot, and the cover of each plant species in each layer was estimated using the seven-level Braun-Blanquet abundance scale.

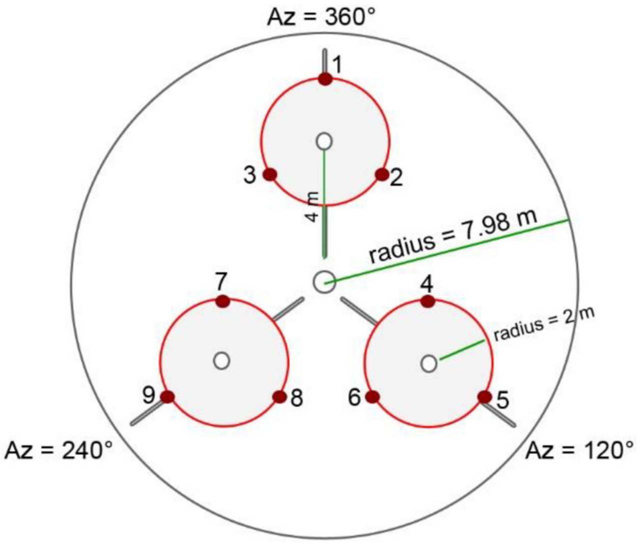

FIGURE 1 Sampling scheme on 0.02 ha circle study plot. The red dot means the soil sample collecting place. Az—azimuth. [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Soil analyses

In the middle of each study plot, a soil pit to a depth of 1 m was dug and then deepened with a soil drill up to 2 m. Subsequently, we examined the soil profile and sampled c.a. 200 g of soil from each genetic horizon to assess the reference soil group following the IUSS Working Group WRB (2015). During this survey, we investigated the presence or absence of plowing horizon to confirm the land use history taken from the Forest Inspectorate data (Figure 2). Afterward, we collected soil samples (ca. 200 g, up to 5 cm depth) and forest litter (FL) in the direct vicinity (c.a. 2 cm) of places where soil samples for mesostigmatid mite investigation were collected (one sample per plot, in total 21 × 2 samples). In each sample, we assessed soil texture

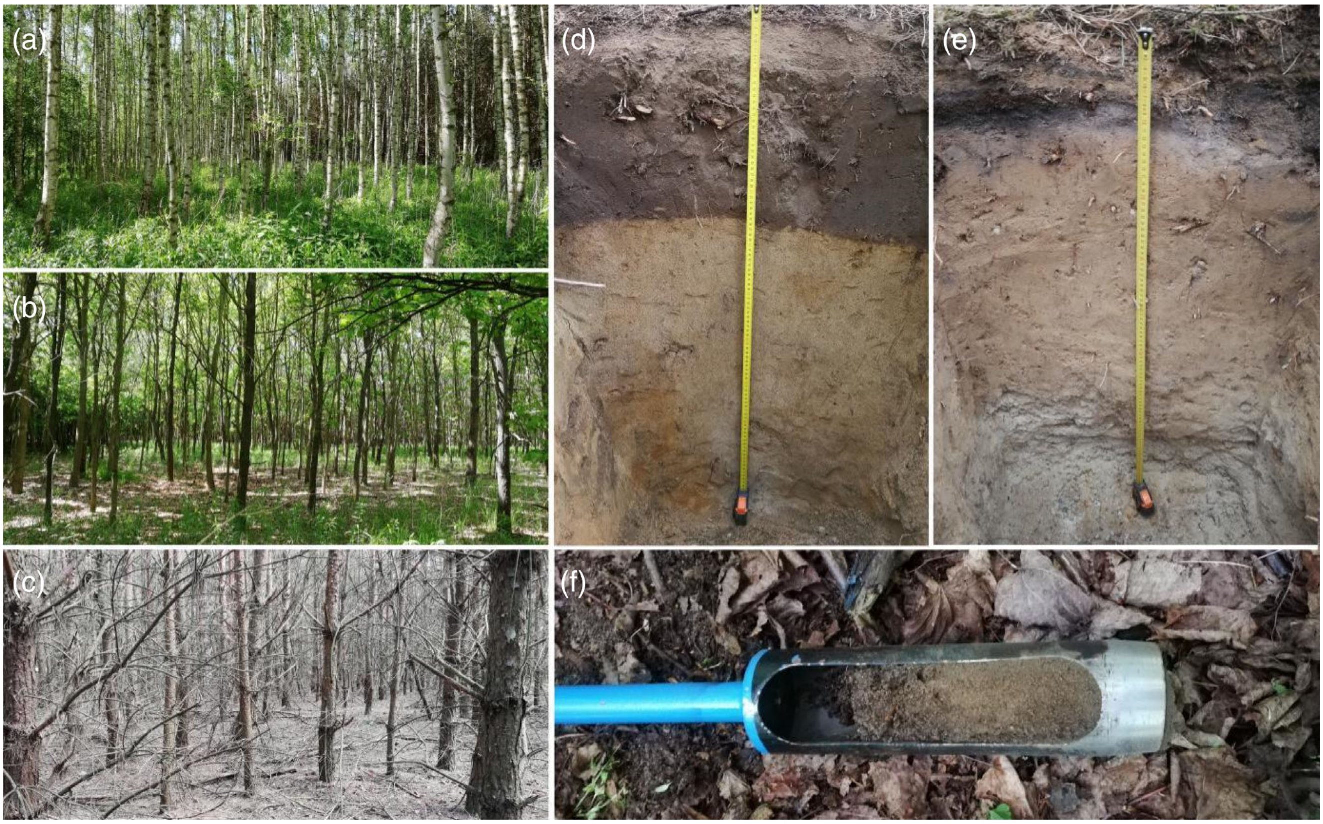

FIGURE 2 Study sites on post-agricultural lands: (a) birch stands, (b) oak stands, (c) pine stands, soil profiles: (d) rusty soil in post-agricultural land under Scots pine, (e) rusty soil in forest land under Scots Pine, soil sample—(f). [Colour figure can be viewed at wileyonlinelibrary.com]

(Casagrande's aerometric method modified by Prószyński); soil organic matter (%), SOM (loss on ignition method); $CaCO_3$ (%) content (Scheibler's method); pH of soil and forest litter in distilled water in a 1:2.5 dry soil:water solution ratio (potentiometric method); total nitrogen (%), N in soil and forest litter (Kjeldahl's method using sulfuric acid and K_2SO_4:$CuSO_4$ catalyst); as well as soil organic carbon (%), SOC (Turin's method) (Hoogsteen et al., 2015; Lityński et al., 1976; Nelson & Sommers, 2018; Warzyński et al., 2018). Furthermore, in soil and litter samples, we investigated the total contents of sodium (%), Na, potassium (%), K, magnesium (%), Mg, calcium (%), Ca, ferrum (mg/kg), Fe, cadmium (mg/kg), Cd, lead (mg/kg), Pb, manganese (mg/kg), Mn, zinc (mg/kg), Zn, and copper (mg/kg), Cu (atomic absorption spectrometry analysis—AAS Varian 55B). Additionally, 21 samples of intact soil (100 cm^3) were taken to assess bulk density (g/cm^3), BD (core method), and soil moisture (%), SM (gravimetric method).

2.3 | Soil fauna studies

In total, 567 soil samples (21 plots × 9 samples × 3 replications) were collected using metal soil corer (ø 5 cm) to a depth of 15 cm. Sampling was carried out in May 2021, October 2021, and May 2022. In the laboratory, soil samples were placed on a Berlese–Tullgren apparatus for 7 days at 30°C. This extraction chamber forces living soil organisms to move away from the heat source to avoid desiccation and fall into ethanol beakers placed below the soil samples. Mesostigmatid mite individuals were removed from the alcohol solution and placed under a binocular microscope and placed in the Hoyer's medium. We identified the specimens using a microscope Zeiss (Zeiss Axio Scope.A1). On this basis, each individual was classified into the appropriate species level or higher taxonomic unit based on the latest specialist literature (Ghilyarov & Bregetova, 1977; Gwiazdowicz, 2007; Karg, 1971, 1993; Mašán & Halliday, 2014; Micherdziński, 1969; Moraes et al., 2022). Rare mite species and their developmental stages were preserved on permanent slides in a liquid medium.

2.4 | Data analysis

Abundance was presented as the mean value per square meter, while species richness was the mean value per plot in each habitat type (land type and tree species) followed by the standard error (SE). Diversity was calculated per plot based on Shannon–Wiener's index; $H' = -\Sigma p_i \ln(p_i)$, where p_i is the proportion of a particular species in the mite community. We applied generalized linear models (GLM), assuming a Tweedie distribution for all examined variables. We used tweedie() function from the statmod package, where the index of power variance function (var.power) and index of power link function (link. power; where 0 produces a log-link, while 1 produces the identity link) were used. Tweedie distribution belongs to the exponential family and is recommended for the variables that are positive values and zeros mixture (Dunn & Smyth, 2018). We applied predictors in models with low variance inflation factors (VIF < 3). Moreover, we conducted Tukey posteriori tests (post-hoc) for each model to determine the differences between the studied habitat types and soil factors. The statistical significance of variables used in GLM was calculated using *t*-values (results were treated as significant when $p < 0.05$). Statistical analyses were done in R software (R Core Team, 2018).

To show the relationships between mesostigmatid mite communities, soil properties, and habitat types (land type and tree species), we conducted canonical correspondence analysis (CCA) implemented in the *vegan package*. The variables included in the conducted CCA final model were based on AIC. Environmental variables were selected on VIF < 2. We conducted a permutational analysis of variance (PERMANOVA) to test the factors. Additionally, we plotted a cumulative species number using the *vegan::specaccum*() function (Oksanen et al., 2018). We used the bipartite package to describe the relationship between each mite taxa and habitats (Dormann et al., 2008), assuming habitat types as lower, whereas mesostigmatid mite taxa as higher-level groups. The taxa-level response to certain habitats was described by the specialization index d', which expresses whether a given taxon is a non-specialist or a perfect specialist (range from 0 (non-specialist) to 1 (perfect specialist)) and is derived from the Kulback–Leibler distance. In addition, index d' describes how strongly specific taxa differ from a random sampling of available interacting partners (Dormann, 2011).

3 | RESULTS

3.1 | Soil properties among habitats

Our study revealed that the pH and thickness of forest litter, SOM, BD, SM, SOC, contents of elements in the soil (K, Zn, Cu, and Mn), as well as in forest litter (Na, K, Fe, Zn, Cu, and Cd) differed among habitats. The lowest pH of forest litter was recorded in pine stands on forest land (4.24 ± 0.27). Interestingly, the content of SOM reached the highest value in the oak stands growing on forest land (4.86 ± 0.32%) and the lowest in oak stands on post-agricultural land (1.93 ± 0.32). The same pattern was noted for SOC content (2.82 ± 0.19% and 1.12 ± 0.19, respectively). The lowest BD was recorded in birch stands on forest land (0.75 ± 0.18). The highest SM was revealed in birch stands growing on forest land (9.99% ± 1.98), while the lowest in pine stands on post-agricultural land (3.15 ± 0.37). The most significant differences were recorded between Fe content in forest litter of beech stands on forest land (the lowest content) and oak on post-agricultural land—the highest content ($df = 6$, $F = 7.215$, $p = 0.001$). Also, Na content in forest litter of pine (highest) and beech (lowest) stands growing on forest land ($df = 6$, $F = 3.371$, $p = 0.029$) differed significantly. Mn content in soil within pine and oak stands on post-agricultural lands were significantly higher than in other examined habitats (df = 6, $F = 37.86$, $p < 0.0001$) (Table 1).

3.2 | Mite abundance, species richness, and diversity

In total, 1355 mesostigmatid mites were classified into 58 taxa (50 taxa identified as species and 8 as genera). Mite abundance was affected by post-agricultural land (Table 2; $p = 0.019$; model details: var.power = 1.8, link.power = 0) and Na content in the forest ($p = 0.042$). Overall, the highest mean abundance was recorded in birch stands growing on forest land (1888.89 ± 240.72 ind./m^2) (Figure 3). Interestingly, the most significant difference in mean abundance was observed between birch stands on forest land and oak stands on post-agricultural land or birch stands on post-agricultural land (df = 6, $F = 7.44$, $p < 0.0001$).

The diversity of mite communities was affected by post-agricultural land (Table 2; $p = 0.004$; model details: var.power = 1.0; link.power = 0) and Na content in the forest litter ($p = 0.005$). Species richness was affected by post-agricultural land ($p > 0.001$; model details: var.power = 1.8, link.power = 0), Na content in forest litter ($p = 0.001$), pine ($p = 0.007$), and oak tree ($p = 0.050$). The highest mean species richness was recorded in oak stands growing on forest land (21.33 species ±2.73). In contrast, the lowest value was found in oak stands on post-agricultural land (9.33 ± 1.86). Similarly, mean diversity was the highest in oak stands on forest land (2.60 ± 0.16) and the lowest in oak stands on post-agricultural land (1.78 ± 0.25). Tukey *posteriori* test showed that species richness significantly differed between oak stands on post-agricultural land and oak and beech stands growing on forest land (df = 6, $F = 268.6$, $p < 0.0001$). Moreover, the species diversity of mesostigmatid mite communities was significantly different between oak stands growing on forest land and post-agricultural land (df = 6, $F = 130.9$, $p < 0.0001$). Cumulative species richness analysis conducted for studied habitats showed a flattering trend of species accrual with increased sampling effort. The curve line for beech stands growing on forest land, and oak stands on post-agricultural land exceeded the curve lines for other examined habitats (Figure 5).

3.3 | Structure of mite communities

Most mites were represented by *Veigaia nemorensis* (C.L. Koch) (165 ind.; 12.2% of all recorded mites), *Zercon peltatus* C.L. Koch (156; 11.5%), and *Paragamasus conus* (Karg) (141; 10.4%). Most mites represented Parasitidae (348 ind.; 25.7%), Zerconidae (205; 15.1%), and Veigaiidae (189; 14.0%) families. Thirty-two species were classified as rare (<10 ind.). The co-occurrence network for bipartite relationships between mesostigmatid mite taxa and studied habitat types revealed that only four mesostigmatid mite taxa—*Hypoaspis aculeifer* (Canestrini), *P. conus* (Karg), *Paragamasus* spp. Athias-Henriot, *V. nemorensis* (C.L. Koch)—were recorded from all seven habitat types, whereas 17 taxa were unique species for a single habitat (Figure 4) (for more details, see Appendix B).

The CCA revealed significant (Table 3) differences in mite taxa distribution along with constrained components. Axes 1 and 2 explained 29.36% and 14.81% of variance, respectively. Moreover, analysis of variance conducted for the model showed that Mg in the litter, pH of the soil, soil K, and soil Pb were significant (Figure 6).

4 | DISCUSSION

Our outcomes can be analyzed and discussed at least in two aspects which include (1) the impact of land use history (long-term agricultural practice in our case) and (2) the impact of tree species on, both soil properties and mesostigmatid mites communities.

Our study revealed that soil properties differ between agricultural and forest rusty soils. We have noticed that five among almost 30 soil parameters (i.e., pH of forest litter, SOC, BD, SM, and Mn content) significantly differed among stands with the same tree species growing on different lands. Agricultural rusty soil had significantly higher values of soil pH, BD, and Mn content, whereas forest rusty soils had higher values of SOC and SM. Our study is in line with Olszewska and Smal (2008) who also revealed that the pH of soil and forest litter in 30 y/o Scots pine stands on post-agricultural sandy soils (Dystric Arenosol) reached higher values. Similarly to our study, they also found higher SOC, but lower N content on forest lands, when compared to agricultural lands. It is worth mentioning that SOC increased with increasing soil acidity in our study. For instance, post-agricultural land had less acidic soil, SOC varied between 1.12% and 1.48%, whereas forest lands had more acidic soil, and SOC varied from 1.66% to 2.82%. This suggests that in a more acidified environment the amount of SOC increases, which is in line with other studies (Kögel-Knabner et al., 2008; Lützow et al., 2006; McIntosh & Allen, 1993). The changes are driven by the plant species which shapes the soil pH by its litter which finally leads to the accumulation of the SOM. This pattern was described for other types of habitats such as coniferous, broadleaved, and mixed forests on various soil types (Devi, 2021; McIntosh & Allen, 1993; Oostra et al., 2006). Therefore our expectations considering the rapid increase of SOC after the afforestation of post-agricultural lands was confirmed. Additionally, Cukor et al. (2017) and Gawęda et al. (2019) proved that the increase in SOC stock and a decrease in soil pH on post-agricultural land is related to increasing stand age. We have recorded that Mn content had the highest value in oak stands growing on post-agricultural land. This is in line with other studies which proved that Mn content in soil may increase in the early phases of afforestation and that oaks have a relatively high accumulation of that micro-element in bark and leaves (Jiménez et al., 2007; Kula et al., 2013; Laskowski et al., 1995).

Considering the impact of certain tree species on the soil environment, we have noticed that eight soil properties (i.e., pH of forest litter, forest litter thickness, Mn in soil, Na, Cd, Fe, Zn, and Cu content

TABLE 1 Soil characteristic of stands.

	Forest land				Post-agricultural land		
Soil properties	**Beech**	**Birch**	**Oak**	**Pine**	**Birch**	**Oak**	**Pine**
pH of FL	5.60 ± 0.08^{a}	5.21 ± 0.03^{a}	4.72 ± 0.40^{bc}	4.24 ± 0.47^{c}	5.68 ± 0.42^{a}	5.18 ± 0.27^{ab}	5.19 ± 0.20^{ab}
FL thick. (cm)	4.53 ± 0.15^{a}	1.63 ± 0.12^{d}	2.37 ± 0.15^{c}	3.60 ± 0.17^{b}	1.77 ± 0.06^{d}	2.47 ± 0.12^{c}	3.50 ± 0.20^{b}
SOM (%)	3.07 ± 1.61^{ab}	3.50 ± 0.58^{ab}	4.86 ± 0.55^{a}	2.86 ± 0.45^{ab}	1.99 ± 0.46^{b}	1.93 ± 0.56^{b}	2.55 ± 0.57^{b}
SOC (%)	1.78 ± 0.93^{ab}	2.03 ± 0.34^{ab}	2.82 ± 0.32^{a}	1.66 ± 0.26^{ab}	1.15 ± 0.27^{b}	1.12 ± 0.33^{b}	1.48 ± 0.33^{b}
BD (g/cm^{3})	1.26 ± 0.21^{abc}	0.75 ± 0.31^{c}	0.90 ± 0.20^{bc}	0.84 ± 0.17^{c}	1.40 ± 0.23^{ab}	1.42 ± 0.04^{ab}	1.44 ± 0.04^{a}
SM (%)	4.69 ± 0.99^{bc}	9.99 ± 3.42^{a}	7.63 ± 0.57^{ab}	5.28 ± 1.42^{bc}	4.84 ± 0.14^{bc}	3.74 ± 0.50^{bc}	3.15 ± 0.63^{c}
Na in FL (%)	0.0020 ± 0.0018^{b}	0.0035 ± 0.0006^{ab}	0.0043 ± 0.0003^{ab}	0.0054 ± 0.0013^{a}	0.0040 ± 0.0006^{ab}	0.0042 ± 0.0009^{ab}	0.0032 ± 0.0004^{ab}
K (%)	0.0035 ± 0.0005^{b}	0.0049 ± 0.0017^{ab}	0.0048 ± 0.0011^{ab}	0.0043 ± 0.0006^{b}	0.0058 ± 0.0010^{ab}	0.0078 ± 0.0020^{a}	0.0063 ± 0.0003^{ab}
K in FL (%)	0.0338 ± 0.0293^{b}	0.0678 ± 0.0093^{ab}	0.0671 ± 0.0134^{ab}	0.0413 ± 0.0048^{ab}	0.0544 ± 0.0110^{ab}	0.0728 ± 0.0075^{a}	0.0502 ± 0.0039^{ab}
Fe in FL (mg/kg)	68.64 ± 59.55^{c}	143.78 ± 31.23^{abc}	159.90 ± 29.19^{ab}	86.75 ± 14.68^{bc}	161.04 ± 19.78^{ab}	219.26 ± 34.72^{a}	129.40 ± 12.90^{abc}
Cd in FL (mg/kg)	0.24 ± 0.21^{c}	0.73 ± 0.17^{ab}	0.51 ± 0.08^{abc}	0.38 ± 0.14^{bc}	0.92 ± 0.26^{a}	0.43 ± 0.03^{bc}	0.49 ± 0.45^{bc}
Mn (mg/kg)	60.31 ± 55.97^{c}	5.04 ± 2.54^{c}	31.31 ± 10.28^{c}	60.50 ± 10.40^{c}	75.42 ± 31.35^{c}	326.68 ± 31.80^{a}	203.71 ± 44.27^{b}
Zn (mg/kg)	4.89 ± 0.46^{b}	2.73 ± 0.65^{b}	6.35 ± 0.78^{ab}	5.11 ± 1.45^{b}	7.49 ± 4.10^{ab}	11.57 ± 3.56^{a}	8.83 ± 1.52^{ab}
Zn in FL (mg/kg)	18.66 ± 16.20^{b}	88.51 ± 0.46^{a}	29.46 ± 0.85^{b}	25.57 ± 3.88^{b}	80.24 ± 18.58^{a}	40.10 ± 10.50^{b}	27.52 ± 6.73^{b}
Cu (mg/kg)	4.89 ± 0.46^{b}	2.73 ± 0.66^{b}	6.35 ± 0.78^{ab}	5.11 ± 1.45^{b}	7.49 ± 4.10^{ab}	11.57 ± 3.56^{a}	8.83 ± 1.52^{ab}
Cu in FL (mg/kg)	18.66 ± 16.20^{b}	88.51 ± 0.46^{a}	29.46 ± 0.8^{5b}	25.57 ± 3.88^{b}	80.24 ± 18.58^{a}	40.10 ± 10.50^{b}	27.52 ± 6.73^{b}

Abbreviations: BD, bulk density; Cd in FL, Cd content in forest litter; Cu in FL, Cu content in forest litter; Cu, Cu content in soil; Fe in FL, Fe content in forest litter; FL thick, forest litter thickness; K in FL, K content in forest litter; K, K content in soil; Mn, Mn content in the soil; Na in FL, Na content in forest litter; pH of FL, pH of forest litter; SM, soil moisture; SOC, soil organic carbon; SOM, soil organic matter content; Zn in FL, Zn content in forest litter; Zn, Zn content in soil.

TABLE 2 Generalized linear mixed models explaining mite abundance, species richness, and Shannon diversity.

	Abundance				Species richness				Diversity			
Predictors	**Estimate**	**SE**	***t* value**	**Pr (>|t|)**	**Estimate**	**SE**	***t* value**	**Pr (>|t|)**	**Estimate**	**SE**	***t* value**	**Pr (>|t|)**
(Intercept)	1.067	8.661	0.123	0.902	−8.055	6.939	−1.161	0.246	−1.220e+01	8.045e+00	−1.516	0.130
Post-agricultural land	−1.515	0.643	−2.355	**0.019**	−1.723	0.519	−3.318	**>0.001**	−1.741e+00	6.006e-01	−2.898	**0.004**
Silver birch	1.127	0.840	1.342	0.180	1.278	0.677	1.887	0.060	1.050e+00	7.529e-01	1.395	0.164
Pedunculate oak	0.878	0.711	1.236	0.217	1.131	0.574	1.970	**0.050**	5.310e-01	8.871e-01	0.599	0.550
Scots pine	0.867	0.577	1.503	0.134	1.268	0.467	2.715	**0.007**	6.570e-01	8.896e-01	0.739	0.461
pH (soil)	0.290	0.353	0.820	0.413	0.065	0.282	0.232	0.817	−5.039e-01	4.639e-01	−1.086	0.278
SOM	0.121	0.146	0.824	0.410	−0.014	0.117	−0.121	0.904	−1.656e-01	1.548e-01	−1.070	0.285
Bulk density	1.066	0.688	1.549	0.122	0.893	0.552	1.618	0.106	1.086e+00	7.186e-01	1.511	0.131
Soil moisture	0.061	0.110	0.564	0.573	0.017	0.085	0.202	0.840	3.807e-03	1.028e-01	0.037	0.970
N (soil)	−0.604	3.291	−0.184	0.854	3.142	2.646	1.187	0.240	6.275e+00	3.756e+00	1.671	0.095
N (litter)	0.189	0.593	0.319	0.750	−0.307	0.479	−0.640	0.522	−4.261e-01	6.414e-01	−0.664	0.507
Mg (soil)	20.569	47.223	0.436	0.663	42.007	37.828	1.110	0.267	9.040e+01	5.485e+01	1.648	0.100
Ca (soil)	−22.960	49.054	−0.468	0.640	−10.180	39.227	−0.260	0.780	−2.953e+01	4.493e+01	−0.657	0.511
Na (soil)	15.628	374.236	0.042	0.967	−46.908	299.129	−0.157	0.875	−5.182e+02	5.468e+02	−0.948	0.344
Na (litter)	−226.605	111.274	−2.036	**0.042**	−297.234	90.531	−3.283	**0.001**	−3.367e+02	1.197e+02	−2.813	**0.005**
K (soil)	−38.333	91.817	−0.417	0.677	−6.690	73.219	−0.091	0.927	−5.522e+00	9.134e+01	−0.060	0.952
K (litter)	−2.542	13.171	−0.193	0.847	6.674	10.548	0.633	0.527	2.136e+01	1.370e+01	1.559	0.120

Note: Bold values present results treated as significant (with $p < 0.05$).
Abbreviation: SE, standard error.

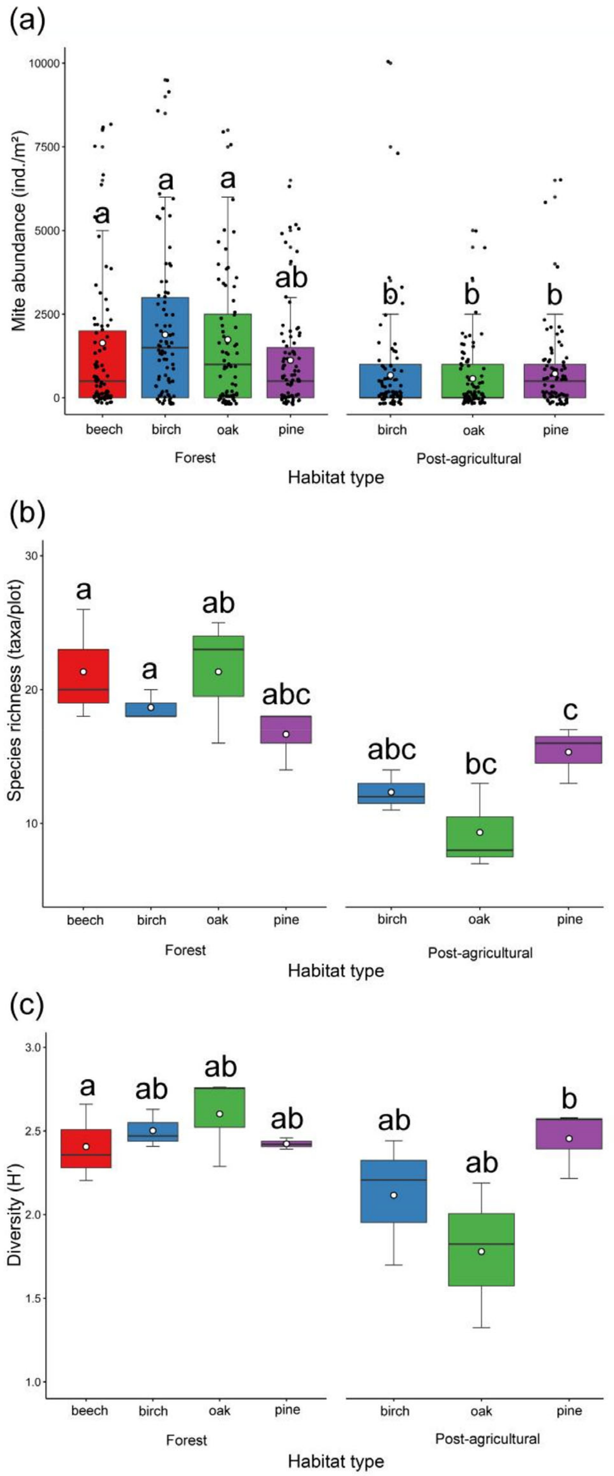

FIGURE 3 Mesostigmatid mite abundance per square meter (a), species richness (b), and diversity (c) were recorded for four tree species between two examined land use types (data presented as mean values). White dots indicate mean values, while black dots in figure A are data points. [Colour figure can be viewed at wileyonlinelibrary.com]

in forest litter) differed among examined stands growing on the same land type. For example, the pH of forest litter in beech stands was higher than in oak and pine stands growing on forest lands (Table 1). Overall, forest litter thickness was the highest in beech when compared to birch stands. Additionally, the content of Zn and Cu was from 3 to 4.7 times higher in the forest litter of the birch stands when compared to other forests growing on forest lands. Moreover, Na content in forest litter differs only between pine and beech stands growing on forest land (Table 1). This may indicate that the impact of tree species is more important for Na content in forest land than previous agricultural practices. The increase of Na concentration in the soil is related to the dispersion of soil colloids and the deterioration of soil structure. This hinders the development of roots and nutrient uptake which is crucial for their growth (Stearns et al., 2005). This outcome can be explained by Marcos et al. (2010), who revealed that the content of Na in the litterfall of oak was lower than in the litterfall of beech and pine.

Our results proved that tree species and agricultural practice shaped the abundance, species richness, and diversity of mesostigmatid mites communities. All mentioned parameters were the highest in forest lands (Figure 3a–c), which was expected. For instance, the highest abundance was recorded in birch stands, while species richness and diversity reached the highest values in oak stands growing on forest land. Further, our study revealed the highest species richness in oak and pine stands on forest land. Surprisingly, abundance, species richness, and diversity were the lowest in oak stands growing on post-agricultural land. This may suggest that the response of certain tree species (oak in our case) may be habitat-specific. Aponte et al. (2012) proved that changes in soil chemistry (pH and Ca content) led to changes in ectomycorrhizal community structure, which may be associated with the structure of decomposed mites communities (Schneider et al., 2005) which play the role of base food for predatory Mesostigmata (Koehler, 1999). Our research on rusty soils revealed that some soil parameters such as Na content in forest litter shaped abundance, species richness, and diversity of mite assemblages. Ji et al. (2020) proved that a slight increase (0.005%) of Na content in the soil may enhance soil fauna abundance and soil extracellular enzyme activity, and finally support the litter decomposition process. However, a larger sodium content increase (0.5%) reduces microbial activity but attracts more soil fauna. Additionally, these authors also proved that an increase in Na content may eliminate the "Home Field Advantage" effect by decreasing selective foraging of soil fauna for different forest litters (Ji et al., 2020). The impact of sodium content on soil fauna may also depend on soil type. For instance, Lóšková et al. (2013) reported that decomposer mite communities (Oribatid mites) inhabiting Dystric Cambisol were resistant to sodium content.

The mite communities in our study were dominated by *V. nemorensis* (∼12% of all recorded mites), *Z. peltatus* (∼11%), and *P. conus* (∼10%). The presence of these species was expected as they are typical forest species (Manu, 2014; Skorupski, 2008; Skorupski et al., 2013). Only four mesostigmatid mite taxa including *Hypoaspis aculeifer*, *P. conus*, *Paragamasus* spp., *V. nemorensis* were noted from all habitat types. *H. aculeifer* is a common pioneer species, occurring in post-agricultural lands and in buffer strips. On the other hand, *V. nemorensis* is also a species commonly found on post-agricultural land and in degraded or post-industrial areas (Skorupski et al., 2013), predominantly in upper soil layers—organic humus and litter. Trophic preferences of *V. nemorensis* are mainly composed of bacterial and

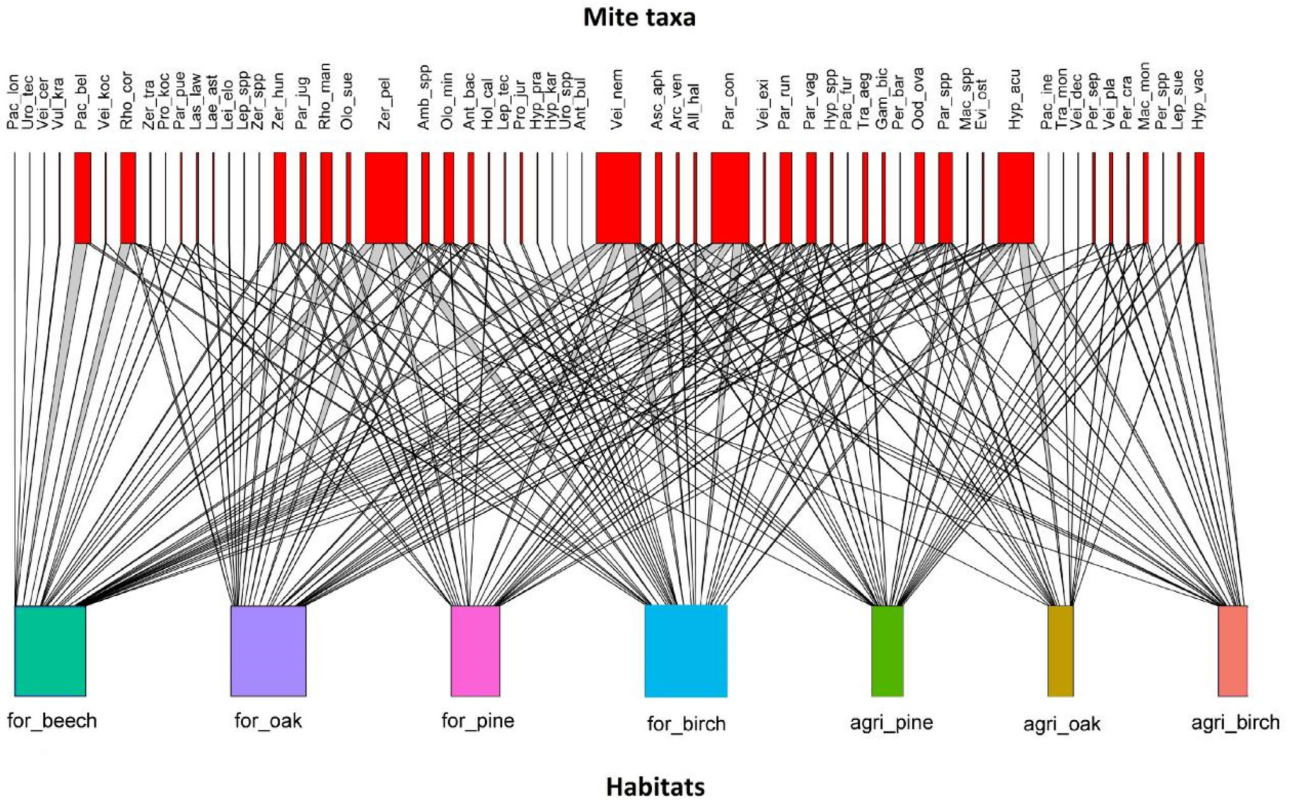

FIGURE 4 Co-occurrence network for bipartite relationships between mesostigmatid mite taxa (upper boxes) and habitat types (lower boxes). Boxes are proportional to total mite abundance, whereas ribbon width is proportional to the proportion of co-occurrence. Abbreviations of mite taxa indicate the first three letters of the genus name and the first three letters of the species name for each mite taxon (for abbreviations of mite taxa see Appendix B). Abbreviations of habitats: for_beech—beech stands on forest land, for_oak—oak stands on forest land, for_pine—pine stands on forest land, for_birch—birch stands on forest land, agri_pine—pine stands on post-agricultural land, agri_oak—oak stands on post-agricultural land, agri_birch—birch stands on post-agricultural land. [Colour figure can be viewed at wileyonlinelibrary.com]

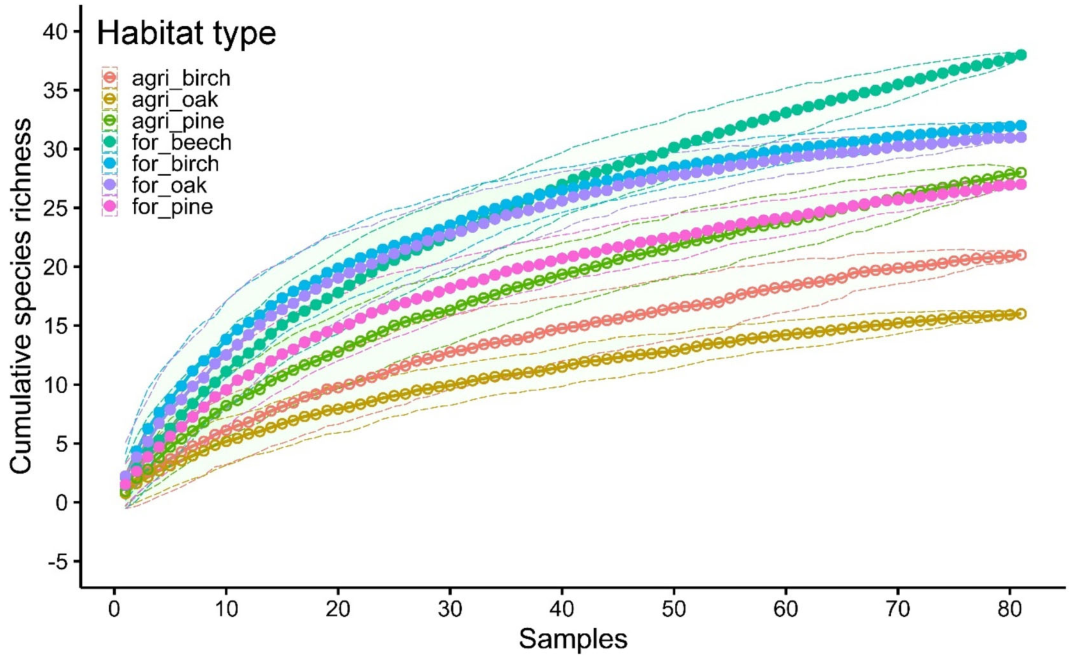

FIGURE 5 Cumulative species richness (data presented as mean values) was recorded for each habitat. Abbreviations of habitats: for_beech—forest_beech, for_oak—forest_oak, for_pine—forest pine, for_birch—forest_birch, agri_pine—post-agricultural_pine, agri_oak—post-agricultural_oak, agri_birch—post-agricultural_birch. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 3 PERMANOVA test of the influence of environmental variables on mite species communities in CCA reduced space.

Predictors	Df	ChiSquare	F	Pr (>F)
MGL	1	0.19141	3388	**0.001**
PHS	1	0.12316	2180	**0.010**
NS	1	0.06542	1158	0.291
FES	1	0.08382	1484	0.147
KS	1	0.14726	2606	**0.002**
BD	1	0.05942	1052	0.376
CAS	1	0.05191	0,919	0.518
PBS	1	0.11930	2112	**0.010**
NAL	1	0.08669	1534	0.085
PHL	1	0.09300	1646	0.068
Residual	10	0.56499	AIC	108.03

Note: Bold values present results treated as significant (with $p < 0.05$). Abbreviations: BD, bulk density; CAS, calcium content in the soil; FES, ferrum content in the soil; KS, potassium content in the soil; MGL, magnesium content in forest litter; NAL, sodium content in the soil; NS, nitrogen content in the soil; PBS, lead content in the soil; PHL, pH of forest litter; PHS, pH of the soil.

root-feeding nematode species (Manu et al., 2017). Additionally, *P. conus* and *Paragamasus* spp. belong to the cosmopolitan family Parasitidae, feeding on eggs and immature stages of other soil-inhabiting microarthropods and nematodes (Kazemi et al., 2013). The presence of these species in post-agricultural soil indicates that the soil started to develop into typical forest soil. However, *Z. peltatus*, as the second most abundantly reported species, was not reported in two habitats—birch and oak stands on post-agricultural lands. This species is nematophagous (Kamczyc et al., 2019), sensitive to heavy metals (Seniczak et al., 1997), and in our study was abundant on forest lands. All these, suggest that this species may be considered as a good bioindicator of the agricultural practice.

5 | CONCLUSIONS

In conclusion, we proved that over 20 years after afforestation, the land use history of the post-agricultural lands is still noticeable in the properties of the soil environment. Chemical and ecological parameters significantly differ between forest and post-agricultural litter and soils (16/30 of studied parameters). Moreover, various tree species may create different conditions for the succession of soil Mesostigmata, which is typical for forest habitats. The highest abundance was recorded in birch stands on forest land, whereas the lowest abundance for oak stands growing on post-agricultural land. A higher diversity of mesostigmatid mites is characteristic of forest land and good evidence of the course of forest succession on post-agricultural land. Interestingly, in oak stands we recorded both the highest diversity of mite communities (forest land) and the lowest on post-agricultural land. Birch or pine afforestation may have a better impact than oak in terms of making the chemical and physical characteristics of the soil. The above observations indicate that by choosing a specific tree species, we can influence the restoration of the forest environment at the soil level.

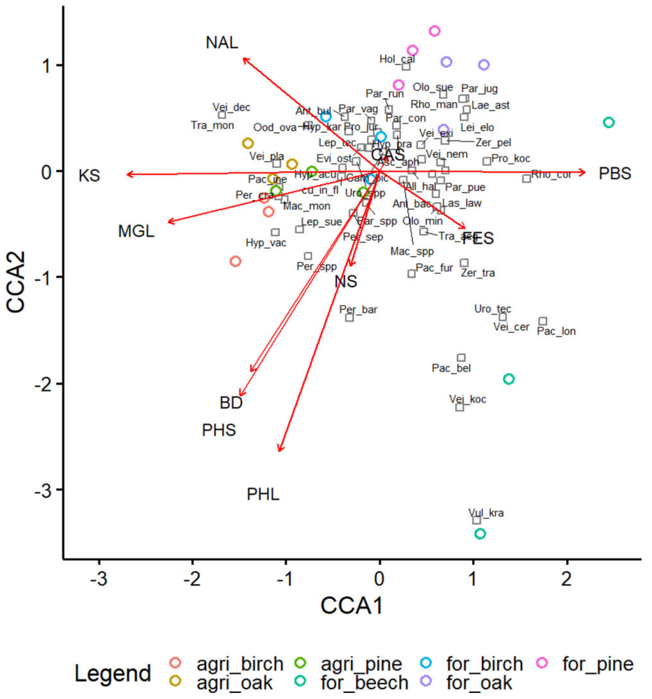

FIGURE 6 Ordination of bi-plot canonical correspondence analysis (CCA) of principal coordinates for Mesostigmata communities occurring in seven habitats. Gray squares show mite taxa labeled with the first three letters of the genus name and the first three letters of the species name for each mite taxon (for abbreviations of mite taxa see Appendix B; see also Table 3 for permutation analysis of variance (PERMANOVA) conducted for final model). Abbreviations of habitats: for_beech—forest_beech, for_oak—forest_oak, for_pine—forest pine, for_birch—forest_birch, agri_pine—post-agricultural_pine, agri_oak—post-agricultural_oak, agri_birch—post-agricultural_birch. Abbreviations of factors: PHS—pH of soil, PHL—pH of litter, SOM—soil organic matter, CDL—cadmium content in forest litter, KS—potassium content in soil, ZNL—zinc content in forest litter, MGL—magnesium content in forest litter. [Colour figure can be viewed at wileyonlinelibrary.com]

CONFLICT OF INTEREST STATEMENT

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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APPENDIX A: STAND CHARACTERISTIC FOR EACH STUDY PLOT

Q. petraea—*Quercus petraea* (Matt) Liebl., *Q. rubra*—*Quercus rubra* L., *B. pendula*—*Betula pendula* Roth., *P. sylvestris*—*Pinus sylvestris* L., *T. cordata*—*Tilia cordata* Mill., *F. sylvatica*—*Fagus sylvatica* L., *F. alnus*—Frangula alnus Mill., *C. arundinacea*—*Calamagrostis arundinacea* (L.) Roth, *S. canadensis*—*Solidago canadensis* L., *V. hederifolia*—*Veronica hederifolia* L., *U. dioica*—*Urtica dioica* L., *G. hederacea*—*Glechoma hederacea* L., *Ch. majus*—*Chelidonium majus* L., *V. myrtillus*—*Vaccinium myrtillus* L., *M. caerulea*—*Molinia caerulea* L., *P. aquilinum*—*Pteridium aquilinum* L. Kuhn., *P. schreberi*—*Pleurozium schreberi* (Willd. ex Brid.) Mitt., *P. juniperinum*—*Polytrichum juniperinum* H.

Number of sample plot	Forest stand	Number of trees (n/ha)	Avg. height (m)	Sd. Height (m)	Total coverage of tree layer (%)	Coverage and species of shrub layer (%)	Coverage and species of vascular ground layer (%)	Coverage and species of bryophytes ground layer (%)
1	*Q. petraea*, *Q. rubra*	1600	12,6	2,6	80	-	*C. arundinacea* [20], *S. canadensis* [10]	-
2	*Q. petraea*, *Q. rubra*	2000	9,2	1,8	80	-	*C. arundinacea* [40], *V. hederifolia* [20]	*P. schreberi* [10]
3	*Q. petraea*, *Q. rubra*	1450	10,3	1,5	70	-	*C. arundinacea* [40], *V. hederifolia* [10]	-
4	*B. pendula*	1550	16,3	2,7	80	-	*S. canadensis* [30], *V. hederifolia* [30], *C. arundinacea* [10], *U. dioica* [10], *G. hederacea* [10]	*P. schreberi* [10]
5	*B. pendula*	2000	16,1	2,0	80	-	*S. canadensis* [30], *V. hederifolia* [30], *U. dioica* [10], *C. arundinacea* [10], *G. hederacea* [10]	*P. schreberi* [10]
6	*B. pendula*	1650	16,2	2,6	80	*F. alnus*	*S. canadensis* [30], *V. hederifolia* [30], *C. arundinacea* [10], *G. hederacea* [10], *U. dioica* [10]	*P. schreberi* [10]
7	*P. sylvestris*	2750	12,4	1,6	90	-	-	*P. schreberi* [30]
8	*P. sylvestris*	2550	12,8	1,3	80	*F. alnus*	*Ch. majus* [10]	*P. schreberi* [30]
9	*P. sylvestris*	2750	13,8	1,1	90	*Frangula alnus*	-	*P. schreberi* [30]
10	*Q. petraea*, *T. cordata*	2250	6,9	1,7	70	*T. cordata*, *Q. petraea*	*V. myrtillus* [10], *M. caerulea* [10]	*P. juniperinum* [40], *P. schreberi* [10]
11	*Q. petraea*, *T. cordata*	2600	7,8	1,1	80	*T. cordata*	*C. arundinacea* [10], *M. caerulea* [10]	*P. juniperinum* [30], *P. schreberi* [20]
12	*Q. petraea*, *T. cordata*	2850	6,4	1,0	80	*T. cordata*	*C. arundinacea* [10], *M. caerulea* [10]	*P. juniperinum* [40], *P. schreberi* [10]
13	*P. sylvestris*	2800	12,5	0,8	90	-	*C. arundinacea* [10]	*P. schreberi* [50], *P. juniperinum* [10]
14	*P. sylvestris*	2600	13,1	1,2	90	-	*C. arundinacea* [10], *P. aquilinum* [10]	*P. schreberi* [50], *P. juniperinum* [20]
15	*P. sylvestris*	2800	13,3	1,1	90	-	-	*P. schreberi* [50], *P. juniperinum* [10]
16	*F. sylvatica*, *B. pendula*	2200	8,7	2,3	100	*F. sylvatica*	-	*P. juniperinum* [20]
17	*F. sylvatica*, *B. pendula*	2400	8,2	1,8	100	*F. sylvatica*, *B. pendula*	-	*P. juniperinum* [20]
18	*F. sylvatica*, *B. pendula*	2250	8,1	1,3	100	*F. sylvatica*	-	*P. juniperinum* [20]
19	*B. pendula*	1850	14,3	1,8	70	*B. pendula*	*P. aquilinum* [40], *C. arundinacea* [30], *V. myrtillus* [20]	*P. juniperinum* [40]
20	*B. pendula*	1550	13,9	1,9	70	*B. pendula*		*P. juniperinum* [30]

Number of sample plot	Forest stand	Number of trees (n/ha)	Avg. height (m)	Sd. Height (m)	Total coverage of tree layer (%)	Coverage and species of shrub layer (%)	Coverage and species of vascular ground layer (%)	Coverage and species of bryophytes ground layer (%)
							V. myrtillus [30], *C. arundinacea* [30], *P. aquilinum* [30]	
21	*B. pendula*	2050	15,3	1,6	80	*B. pendula*, *F. alnus*	*C. arundinacea* [40], *V. myrtillus* [30], *P. aquilinum* [20]	*P. juniperinum* [40]

APPENDIX B: NETWORK STATISTICS FOR MESOSTIGMATID MITE TAXA, DESCRIBING THEIR AFFILIATION TO HABITATS AND SPECIALIZATION

No.	Mite taxa	Abbreviation	Number of habitats	Proportion of habitats	Species specificity index d’
1	*Prozercon kochi* (Sellnick, 1943)	Pro_koc	2	0.65	0.05
2	*Zercon hungaricus* (Sellnick, 1958)	Zer_hun	4	0.42	0.10
3	*Zercon peltatus* C.L.Koch, 1836	Zer_pel	5	0.35	0.09
4	*Zercon triangularis* (C.L.Koch, 1836)	Zer_tri	2	0.69	0.09
5	*Zercon* spp. (C.L.Koch, 1836)	Zer_spp	1	1.00	0.13
6	*Holoparasitus calcaratus* (C.L.Koch, 1839)	Hol_cal	2	0.66	0.17
7	*Leptogamasus suecicus* (Trägårdh, 1936)	Lep_sue	2	0.65	0.36
8	*Leptogamasus tectegynellus* (Athias Henriot, 1967)	Lep_tec	1	1.00	0.25
9	*Leptogamasus* spp. (Trägårdh, 1936)	Lep_spp	1	1.00	0.13
10	*Paragamasus conus* (Karg, 1971)	Par_con	7	0.31	0.07
11	*Paragamasus jugincola* (Athias Henriot, 1967)	Par_jug	4	0.42	0.11
12	*Paragamasus runcatellus* (Berlese, 1903 sensu Karg, 1971)	Par_run	6	0.42	0.17
13	*Paragamasus vagabundus* (Karg, 1968)	Par_vag	6	0.30	0.09
14	*Paragamasus puerilis* (Karg, 1963)	Par_pue	3	0.54	0.11
15	*Paragamasus* spp. (Hull, 1918)	Par_spp	7	0.18	0.06
16	*Pergamasus crassipes* (Linnaeus, 1758)	Per_cra	3	0.49	0.26
17	*Pergamasus barbarus* (Berlese, 1904)	Per_bar	2	0.65	0.11
18	*Pergamasus septentrionalis* (Oudemans, 1902)	Per_sep	3	0.56	0.25
19	*Pergamasus* spp. (Berlese, 1903)	Per_spp	2	0.65	0.17
19	*Vulgarogamasus kraepelini* (Berlese, 1904)	Vul_kra	1	1.00	0.24
20	*Antennoseius bacatus* Athias-Henriot, 1961	Ant_bac	5	0.41	0.07
21	*Antennoseius bullitus* Karg, 1969	Ant_bul	1	1.00	0.00
22	*Arctoseius venustulus* (Berlese, 1917)	Arc_ven	5	0.41	0.06
23	*Asca aphidioides* (Linnaeus, 1758)	Asc_aph	5	0.47	0.09
24	*Gamasellodes bicolor* (Berlese, 1918)	Gam_bic	6	0.25	0.04
25	*Lasioseius lawrencei* (Evans, 1958)	Las_law	3	0.49	0.07
26	*Leioseius elongatus* Evans, 1958	Lei_elo	1	1.00	0.20
27	*Proctolaelaps juradeus* (Schweizer, 1949)	Pro_jur	1	1.00	0.29
28	*Alliphis halleri* (Canestrini & Canestrini, 1881)	All_hal	5	0.41	0.06
29	*Eviphis ostrinus* (C.L.Koch, 1836)	Evi_ost	4	0.40	0.12
30	*Hypoaspis vacua* (Michael, 1891)	Hyp_vac	3	0.68	0.46
31	*Hypoaspis aculeifer* (Canestrini, 1883)	Hyp_acu	7	0.20	0.15
32	*Hyposapis praesternalis* (Willmann, 1949)	Hyp_pra	1	1.00	0.11
33	*Laelaspis astronomica* (C.L.Koch, 1839)	Lae_ast	1	1.00	0.25
34	*Hypoapsis karawaiewi* (Berlese, 1903)	Hyp_kar	1	1.00	0.00
35	*Hypoaspis* spp. (Canestrini, 1884)	Hyp_spp	6	0.37	0.04
36	*Macrocheles montanus* (Willmann, 1951)	Mac_mon	5	0.57	0.29
37	*Macrocheles* spp. (Latreille, 1829)	Mac_spp	2	0.70	0.19
38	*Pachylaelaps bellicosus* (Berlese, 1920)	Pac_bel	2	0.78	0.34
39	*Pachylaelaps furcifer* (Oudemans, 1903)	Pac_fur	2	0.65	0.09
40	*Pachylaelaps ineptus* Hirschmann & Krauss 1965	Pac_ine	1	1.00	0.17
41	*Olopachys suecicus* (Sellnick, 1950)	Olo_sue	4	0.55	0.16

No.	Mite taxa	Abbreviation	Number of habitats	Proportion of habitats	Species specificity index d'
42	*Pachylaelaps longisetis* (Halbert, 1915)	Pac_lon	1	1.00	0.14
43	*Amblyseius* spp. (Berlese, 1904)	Amb_spp	6	0.44	0.07
44	*Rhodacarus coronatus* (Berlese, 1921)	Rho_cor	5	0.67	0.23
45	*Rhodacarus mandibularis* (Berlese, 1921)	Rho_man	5	0.58	0.19
46	*Veigaia cerva* (Kramer, 1876)	Vei_cer	1	1.00	0.02
47	*Veigaia decurtata* (Athias Henriot, 1961)	Vei_dec	1	1.00	0.21
48	*Veigaia exigua* (Berlese, 1916)	Vei_exi	4	0.38	0.10
49	*Veigaia kochi* (Trägårdh, 1901)	Vei_koc	2	0.75	0.16
50	*Veigaia nemorensis* (C.L.Koch, 1839)	Vei_nem	7	0.26	0.02
51	*Veigaia planicola* (Berlese, 1892)	Vei_pla	4	0.41	0.25
52	*Trachytes aegrota* (C.L.Koch, 1841)	Tra_aeg	5	0.39	0.14
53	*Trachytes montana* Willmann, 1953	Tra_mon	1	1.00	0.21
54	*Urodiaspis tecta* (Kramer, 1876)	Uro_tec	1	1.00	0.02
55	*Oodinychus ovalis* (C.L.Koch, 1839)	Ood_ova	2	0.71	0.34
56	*Olodiscus minima* (Kramer, 1882)	Olo_min	6	0.34	0.04
57	*Uropoda* spp. (Latreille, 1806)	Uro_spp	1	1.00	0.00

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RESEARCH ARTICLE

WILEY

Environmental role of different-aged pine and oak stands growing on post-agricultural and forest lands in forming the Mesostigmata mites communities

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Abstract

Reclamation of agricultural soil and forest succession after afforestation proceeds slowly and at many levels. Therefore, the history of land use is recorded in the soil's physical, chemical and ecological parameters for many decades. This process depends on time and the form of afforestation, which primarily includes tree species. In our study, we analyzed differences in the physical and chemical characteristics of pine and oak stands on forest and post-agricultural land at 22, 42 and 62 y/o. Our study revealed that 14 of 24 examined parameters (litter pH, soil pH, litter thickness, soil organic matter, C_{org}, bulk density, C/N ratio, soil moisture, soil K, Mg and Mn content, N and Ca litter content, Mg litter content) differed significantly among examined habitats (land use, stand age and tree species). We calculated the abundance, species richness and diversity of the mite communities (Acari, Mesostigmata) for each habitat type. In total, 6730 mites were classified into 72 taxa (60 species, 11 genera and one taxon as family). The highest abundance was recorded in 42 y/o. oak stands on post-agricultural land, while the lowest is in 22 y/o. pine and oak stands on post-agricultural land. The highest species richness and diversity were recorded in the oldest oak stand on post-agricultural land. In contrast, the lowest diversity was recorded in the youngest oak and pine stands on post-agricultural land. Our results demonstrate that the negative impact of the agricultural history of land use weakens over time and provides a better understanding of land use history on the relations between the soil environment and soil fauna, including mesostigmatid mite assemblages.

KEYWORDS

Acari, afforestation, forest biodiversity, forest soil, Mesostigmata, post-agricultural land, soil fauna

1 | INTRODUCTION

Forest stands growing on former agricultural land are present throughout Europe (De Frenne et al., 2011), either as a result of afforestation or spontaneous natural succession (Fayet et al., 2022; Krawczyk, 2015). In Poland, afforestation of post-agricultural lands was commonly carried out under the National Programme for Expanding of Forest Cover on the weakest soils, where agricultural use had been abandoned (Kaliszewski, 2016). As a result, Poland's forest cover increased from 20.8% to 29.5% between 1945 and 2016 (Augustyniuk-Kram & Kram, 2020). The land use history of these areas includes deforestation and long-standing agricultural practices that have resulted in severe soil degradation and reduced biodiversity of soil fauna (Ponge et al., 2013). For this reason, post-agricultural land is considered difficult for afforestation, especially due to poor soil quality, high nitrogen content, low carbon content and higher pH levels. In addition, the growth of trees is limited by the presence of a plough layer, which impedes the penetration of water and roots into the soil profile (Szujecki, 1990).

Post-agricultural land has historically been afforested primarily with Scots pine (*Pinus sylvestris* L.) as a pioneer species. In managed forests, oak (*Quercus robur* L.) is also widely used to afforest former agricultural lands (Bernacki, 1990). Previous research indicated that each of these tree species has a slightly different effect on topsoil, for example, through different carbon concentrations in the forest floor (Podrázský et al., 2009; Vesterdal et al., 2002). This influence can also be dependent on the stand age. Given the above, tree species and stand age shape the conditions of the soil environment and the communities of soil organisms. Forests growing on post-agricultural land are characterized by lower biodiversity than relict forests. It applies to the composition of undergrowth plants (Flinn & Vellend, 2005) and the species composition of soil fauna communities (Gormsen et al., 2006; Harta et al., 2020; Scheu et al., 2003). Harta et al. (2020) demonstrated that springtail communities are less diverse in stands growing on former farmland than in relict forests. Further, Delcourt et al. (2023) revealed that the effect of agricultural land use history on microarthropod abundance depends on pedoclimatic conditions and it decreases with the age of stands. In addition, the authors have shown that mites and springtails are good bioindicators of land use history and pedoclimatic conditions of forest soils. As an example, predatory mites of the Mesostigmata order (Mesostigmata = Gamasida) play the role of bioindicators of environmental conditions, indicating anthropogenic and natural disturbances and perturbations (Kamczyc et al., 2019). Mesostigmatid mites, mainly as predators, prey on soil fauna assemblages such as nematodes, springtails, enchytraeids, insect larvae and other mites (Koehler, 1999). In this way, mesostigmatid mites have an important position in the soil food webs, contributing significantly to the flow of energy and turnover of matter (Ruf & Beck, 2005) and may indirectly induce a strong influence on decomposition dynamics (Urbanowski et al., 2021). Ultimately, the abundance of mesostigmatid mites depends on the dynamics of their prey, which may have different sensitivities to soil environmental conditions (Kamczyc et al., 2019). Despite this, there has been little research in Europe on the afforestation of former agricultural land using mesostigmatid mites as bioindicators (Malica et al., 2022).

Our study aimed to examine the influence of land-use history and tree species in the chronosequence of tree age on both soil chemical parameters and mesostigmatid mite assemblages. We compared pine (*P. sylvestris* L.) and oak (*Q. petraea* (Matt.) Liebl) stands of 22, 42 and 62 y/o., growing on post-agricultural and forest land. We assumed that (1) post-agricultural land would differ from forest land in terms of soil and litter characteristics (e.g., pH, C/N, soil organic matter [SOM], bulk density) and would be shaped differently by pine and oak stands. Furthermore, we assumed that (2) differences in soil properties between post-agricultural and forest land would decrease with stand age, as well as (3) age of stand and land use history having an impact on mite communities rather than tree species. Moreover, (4) abundance, species richness and diversity of soil mite communities on post-agricultural land would be most similar to forest land in the oldest, both in pine and oak stands.

2 | MATERIALS AND METHODS

2.1 | Study site and experiment design

The research was conducted in the Opole Forest District (southwestern Poland; 50°83′93″ N, 17°44′53″ E). In this area, large-scale afforestation on former agricultural land has been carried out over the last few decades. The mean forest age in the forest complex where the research was conducted was 59 y/o. The average annual precipitation for research location is ~603 mm, and the average annual temperature reaches ~ +8°C. The vegetation season lasts for ~227 days. Forest vegetation coverage of an investigated area is about 17%. Scots pine (*P. sylvestris* L.) is a predominant forest tree species, accounting for 73% of area and timber resources share. The average age of forest stands is 62 years, and the average volume of growing stock is 313 m^3/ha. Shrub layer mostly consists of *Frangula alnus* Mill., *Sorbus aucuparia* L., *Prunus padus* L. and *Picea abies* (L.) H. Karst while forest floor is mainly covered by *Vaccinium myrtillus* L., *Calamagrostis arundinacea* (L.) Roth., *Pteridium aquilinum* (L.) Kuhn and mosses: *Pleurozium schreberi* (Willd. ex Brid.) Mitt., *Polytrichum juniperinum* Hedw. The altitude interval of the area is between 145 and 190 m asl (Forest Management Plan for Opole Forest Division, 2014). The soils within the study area are dominated by rusty soils (Arenosols acc. to IUSS Working Group WRB, 2022)—45.3%, which are the most common soils in stands managed by Forest States in Poland (Rutkowski et al., 2021).

A total of 36 study plots (2 land types [land, post-agricultural] × 2 tree species [pine, oak] × 3 age classes [22, 42, 62 y/o.] × 3 plots) were established in pine and oak stands growing on post-agricultural and forest land. The size of a single circle sample plot was 0.02 ha (radius = 7.98 m). To avoid pseudoreplication and maintain similarity between microhabitat and soil conditions, the minimal distance between the plots was ~30 m.

2.2 | Soil analyses

The first step was to dig 1 m deep soil pits in the centre of each plot, which we then deepened with a soil drill up to 2 m. Then, we examined the soil profiles (Figure 1) and sampled c.a. 200 g of soil from each genetic horizon to assess the reference soil group following the IUSS Working Group WRB (2022). The presence or absence of ploughing horizon confirmed the land use history (forest/

FIGURE 1 Soil profiles: (a) Post-agricultural land (visible plough layer); (b) forest land. [Colour figure can be viewed at wileyonlinelibrary.com]

post-agricultural) taken from the Forest Inspectorate data. Subsequently, we collected soil samples (ca. 200 g, up to 5 cm depth) and forest litter (FL) in the direct vicinity (c.a. 2 cm) of places where soil samples for mesostimatid mite communities investigation were collected (one sample per plot, in total 36 × 2 samples). In each sample, we assessed soil texture (Casagrande's aerometric method modified by Prószyński); SOM (%), SOM (loss on ignition method); $CaCO_3$ (%) content (Scheibler's method); pH of the soil and forest litter in distilled water in a 1:2.5 dry soil: water solution ratio (potentiometric method); total nitrogen (%), N in soil and forest litter (Kjeldahl's method using sulphuric acid and K_2SO_4:$CuSO_4$ catalyst), as well as soil organic carbon (%), SOC (Turin's method) (Hoogsteen et al., 2015; Lityński et al., 1976; Nelson & Sommers, 2018; Warzyński et al., 2018). Furthermore, in soil and litter samples, we investigated the total contents of sodium (%), Na, potassium (%), K, magnesium (%), Mg, calcium (%), Ca, ferrum (mg/kg), Fe, manganese (mg/kg), Mn, zinc (mg/kg), Zn (atomic absorption spectrometry analysis—AAS Varian 55B). Furthermore, 36 samples of intact soil (100 cm^3) were taken to assess bulk density (g/cm^3), BD (core method) and, soil moisture (%), SM (gravimetric method) (Appendix A).

2.3 | Mesostigmatid mite investigation

In total, 1296 soil samples (36 plots × 9 samples × 4 replications) were collected using metal soil corer (ø = 5 cm) to a depth of 15 cm. Sampling was carried out in July 2021, October 2021, July 2022 and October 2022. Each soil sample was labelled, placed and secured in-to the plastic bag and transported to the Poznań University of Life Sciences. In the laboratory, soil samples were placed on a Berlese-Tullgren apparatus for 7 days at ~30°C (temperature measured at apparatus strainer). The extraction chamber illuminates the samples, forcing soil organisms to move towards the 80% ethanol beakers placed underneath. Mesostigmatid mite individuals were collected from the alcohol solution under a binocular microscope and placed in the Hoyer's medium. A microscope (Zeiss Axio Scope.A1) was used to identify the specimens. All individuals were classified into the appropriate species level or higher taxonomic unit based on the specialist literature (Ghilyarov & Bregetova, 1977; Gwiazdowicz, 2007; Karg, 1971, 1993; Mašán & Halliday, 2014; Micherdziński, 1969; Moraes et al., 2022).

2.4 | Data analysis

All statistical analyses were conducted using R software (R version 4.1.2; R Core Team, 2018). Abundance, species richness and diversity were calculated to mean values followed by the standard error (SE). We presented abundance as the mean value per square meter, while species richness and diversity as mean value per plot in each habitat type (land type, stands age and tree species). We calculated diversity per plot based on Shannon-Wiener's index; $H' = -\Sigma p_i \ln(p_i)$, where p_i is the proportion of a particular species in the mite community. Prior to the model's analysis, the variable distribution was tested using the Shapiro–Wilk test. In order to compare the data that is not measured in the same way we used the *scale()* function to centre and scale the columns of a numeric data matrix. We assumed normal distributions for mite abundance, species richness and Shannon-Wiener's index. In the conducted models (linear mixed-effects models [LMM]), we accounted for random effects connected with collected sample dependencies (study plot), to exclude plot-specific factors, which could bias the inference. Models were developed using the *lme4* package (Bates et al., 2015). Predictors in models were applied with low variance inflation factors (VIF < 3). Furthermore, Tukey posteriori tests (post hoc) were conducted for each model to determine the differences between the soil properties and habitat types. The statistical significance of variables used in LMM was calculated using t-values (results were treated as significant when $p < 0.05$).

We applied canonical correspondence analysis (CCA) implemented in the *vegan* package to show the relationships between mesostigmatid mite communities, soil properties and habitat types (land type, stand age and tree species). The variables included in the conducted CCA final model were based on akaike information criterion (AIC), while environmental variables were selected on VIF <2. A permutational analysis of variance (PERMANOVA) was used to test the used factors. Cumulative species number was conducted and plotted using the *vegan::specaccum()* function (Oksanen et al., 2018). The bipartite package described the relationship between each mite taxa and examined habitats (Dormann et al., 2008), assuming mesostigmatid mite taxa as higher-level, whereas habitat types as lower groups. We described the taxa-level response to certain habitat types by the specialization index *d′*. The index expresses whether a given taxon is a non-specialist or a perfect specialist (range from 0 [non-specialist] to 1 [perfect specialist]) and is derived from the Kulback-Leibler distance (Dormann, 2011).

3 | RESULTS

3.1 | Soil properties among habitats

Soil parameters were analysed in relation to land use history, tree species and stand age. Mean values of soil and litter pH were similar for post-agricultural (soil pH = 3.88 ± 0.07; litter pH = 4.52 ± 0.16) and forest land (3.54 ± 0.06; 4.49 ± 0.13). Litter thickness was higher on forest land (4.81 cm ± 0.39) than on post-agricultural land (2.92 ± 0.14). Similarly, higher values of SOM (4.07% ± 0.35 vs. 2.03% ± 0.13) and C/N ratio (15.22 ± 1.25 vs. 13.45 ± 1.67) were revealed for forest land. Concerning the age of stands, SOM was the highest at 42 y/o. stands (3.90% ± 0.56). In addition, our data revealed an increase in the C/N ratio with the age of the stands (from 11.58 ± 2.04 to 17.10 ± 2.00). Forest litter pH decreased with stand age, which was particularly visible in pine stands growing on post-agricultural land (from 4.68 ± 0.12 to 3.39 ± 0.05). Oak stands achieved higher values of litter pH (5.00 ± 0.05 vs. 4.01 ± 0.11) and SOM (3.44% ± 0.38 vs. 2.66% ± 0.32) compared to pine stands, while C/N ratio was higher for pine stands (16.21 ± 1.61 vs. 12.46 ± 1.20) (Appendix A).

Our study revealed that 14 parameters (litter pH, soil pH, litter thickness, SOM, C_{org}, bulk density, C/N ratio, soil moisture, soil K, Mg and Mn content, litter N and Ca content, litter Mg content) differed significantly among habitats (Appendix C). Conducted Tukey HSD test for the above soil parameters revealed that, i.a. the lowest value of pH of forest litter was noticed in the 62 y/o. pine stand on post-agricultural land (3.39 ± 0.05) and differed significantly from the highest in 22 y/o. oak stand on post-agricultural land (5.18 ± 0.15) (Appendix C). Essentially, the lowest pH of soil was reported in the 22 y/o. oak stand on forest land (3.36 ± 0.10), while the highest in the 22 y/o. oak stand on post-agricultural land (4.33 ± 0.02). The lowest forest litter thickness was recorded in the 62 y/o. oak stand on post-agricultural land (2.1 cm ± 0.1) and the highest in the 42 y/o. pine stand on forest land (7.23 cm ± 0.15). The content of SOM reached the highest value in the 42 y/o. oak stand on forest land (6.13% ± 0.30), while the highest C_{org} content was noticed in the 42 y/o. pine stand on forest land (3.85% ± 0.16). The 22 y/o. pine stand on post-agricultural land was characterized by the highest value of bulk density (1.49 g/cm^3 ± 0.03), as well as the lowest values of the following parameters: SOM (1.44% ± 0.19), C_{org} (0.84% ± 0.11), C/N ratio (5.97 ± 0.66), soil moisture (2.33% ± 0.77) and K content in soil (0.008% ± 0.003). The highest value of C/N ratio was reported at 62 y/o. pine stand on forest land (23.95 ± 1.79). In conclusion, the C/N ratio increased with the age of pine stands, while it decreased in oak stands. This was revealed for both studied types of land use. Bulk density (0.66 g/cm^3 ± 0.09), N content in forest litter (1.149% ± 0.137), K content in forest litter (0.009% ± 0.0001) and Mg content in forest litter (0.012% ± 0.001) reached the lowest values in the 42 y/o. pine stand on forest land. The contents of Mn, Mg and K in soil and Mg in litter were higher in the youngest stands—regardless of tree species and type of land use. In the case of a pine stand on forest land, there was a marked decrease in Na content in litter with stand age. Another interesting result is the significant variation in Ca content in forest litter among habitat types, with no significant differences in soil. The exception is a 42 y/o. pine stand on forest land, which differed significantly in Ca content in soil from all other stands.

3.2 | Mite abundance, species richness and diversity

In total, 6730 individuals were classified into 72 taxa (60 species, 11 genera, one taxon as family). The analysis (Table 1) revealed that mite abundance was influenced by bulk density ($p = 0.016$), litter pH ($p = 0.041$), litter content of N ($p = 0.037$) and Na ($p = 0.009$) and soil content of Zn ($p = 0.048$). Generally, comparing land types our data revealed higher mean mite abundance was recorded in forest land compared to post-agricultural land (2841.05 ind./m^2 ± 122.19 vs. 2351.85 ± 122.86). Additionally, the highest abundance (3847.22 ± 356.14 ind./m^2) was noticed in 42 y/o. oak stand growing on post-agricultural land, while the lowest in 22 y/o. pine (685.19 ± 115.55) and oak (699.07 ± 104.20) stands on post-agricultural land (Figure 2a).

The analysis revealed that species richness was influenced by Mn content in soil ($p = 0.032$) (Table 1). The highest species richness was recorded in the oldest oak stand on post-agricultural land (32.33 species ±3.28), whereas lower in the youngest oak (13.67 ± 1.76) and pine (14.00 ± 1.15) stands on post-agricultural land (Figure 2b). The same tendency was recorded for diversity of mite communities, which was the highest in the 62 y/o. oak stand on post-agricultural land (2.92 ± 0.08) and the lowest in the 22 y/o. oak (2.14 ± 0.13) and pine

TABLE 1 Linear mixed-effects models explaining mite abundance, species richness, and Shannon-Wiener diversity.

Abundance					Species richness					Diversity				
Predictors	Estimates	SE	CI	*p*	Predictors	Estimates	SE	CI	*p*	Predictors	Estimates	SE	CI	*p*
(Intercept)	0.11	0.64	−1.29 to 1.52	0.861	(Intercept)	−0.27	0.57	−1.50 to 0.95	0.641	(Intercept)	−0.18	0.56	−1.35 to 0.99	0.753
Land	−0.50	0.84	−2.35 to 1.34	0.561	Stand age	0.14	0.32	−0.55 to 0.83	0.672	Soil texture	0.14	0.55	−1.01 to 1.29	0.799
Tree	−1.05	0.70	−2.60 to 0.50	0.163	Tree	−0.62	0.45	−1.59 to 0.36	0.194	pH (soil)	0.03	0.20	−0.38 to 0.44	0.867
Soil texture	0.59	0.46	−0.43 to 1.60	0.228	Soil texture	0.63	0.61	−0.67 to 1.93	0.317	Bulk density	0.27	0.19	−0.13 to 0.68	0.174
pH (litter)	−0.79	0.34	−1.53 to −0.04	**0.041**	Litter thickness	0.06	0.36	−0.71 to 0.82	0.880	Soil moisture	−0.24	0.20	−0.66 to 0.17	0.239
Litter thickness	0.41	0.36	−0.38 to 1.21	0.276	pH (soil)	0.26	0.23	−0.24 to 0.75	0.282	Zn (litter)	−0.42	0.27	−0.99 to 0.15	0.138
pH (soil)	0.12	0.18	−0.27 to 0.51	0.510	C/N ratio	0.17	0.23	−0.31 to 0.66	0.455	Fe (soil)	0.20	0.26	−0.34 to 0.74	0.452
SOM	0.33	0.29	−0.31 to 0.97	0.281	Bulk density	0.30	0.21	−0.16 to 0.76	0.178	K (soil)	−0.22	0.19	−0.63 to 0.18	0.268
Bulk density	0.53	0.18	0.12– to 0.93	**0.016**	Soil moisture	−0.09	0.22	−0.55 to 0.38	0.691	K (litter)	−0.21	0.21	−0.65 to 0.24	0.345
Soil moisture	0.15	0.17	−0.23 to 0.53	0.397	Zn (litter)	0.15	0.35	−0.61 to 0.91	0.677	Na (soil)	0.04	0.21	−0.41 to 0.48	0.867
N (litter)	1.04	0.44	0.08– to 2.00	**0.037**	**Mn (soil)**	−0.92	0.38	−1.74 to −0.09	**0.032**	Na (litter)	0.11	0.23	−0.37 to 0.58	0.650
Zn (soil)	−0.96	0.43	−1.92 to −0.01	**0.048**	Fe (soil)	0.21	0.29	−0.40 to 0.83	0.466	Ca (soil)	0.12	0.28	−0.48 to 0.71	0.687
Zn (litter)	0.33	0.27	−0.27 to 0.92	0.255	Fe (litter)	0.01	0.26	−0.54 to 0.56	0.959	Ca (litter)	0.26	0.27	−0.30 to 0.81	0.351
Mn (soil)	0.11	0.41	−0.80 to 1.02	0.789	K (soil)	−0.01	0.25	−0.54 to 0.53	0.982					
Fe (soil)	0.03	0.24	−0.51 to 0.56	0.919	K (litter)	−0.26	0.23	−0.75 to 0.23	0.273					
Fe (litter)	0.62	0.45	−0.36 to 1.61	0.191	Na (soil)	0.14	0.27	−0.44 to 0.72	0.610					
K (soil)	−0.15	0.18	−0.55 to 0.24	0.408	Na (litter)	0.25	0.24	−0.27 to 0.77	0.319					
K (litter)	−0.28	0.18	−0.68 to 0.12	0.153	Ca (soil)	0.13	0.35	−0.61 to 0.88	0.709					
Na (soil)	−0.26	0.22	−0.74 to 0.22	0.257	Ca (litter)	0.24	0.33	−0.46 to 0.94	0.477					
Na (litter)	0.73	0.23	0.23–1.24	**0.009**										
Ca (soil)	0.49	0.29	−0.14 to 1.12	0.112										
Ca (litter)	−0.13	0.27	−0.72 to 0.46	0.641										
Random effects					**Random effects**					**Random effects**				
Marginal R^2/conditional R^2			0.610/0.818		Marginal R^2/conditional R^2			0.528/0.603		Marginal R^2/conditional R^2			0.242/0.664	
AIC			123.178		AIC			130.372		AIC			124.936	

Note: Bold values indicate significance.

Abbreviations: AIC, akaike information criterion; CI, confidence intervals; SE, standard error; SOM, soil organic matter.

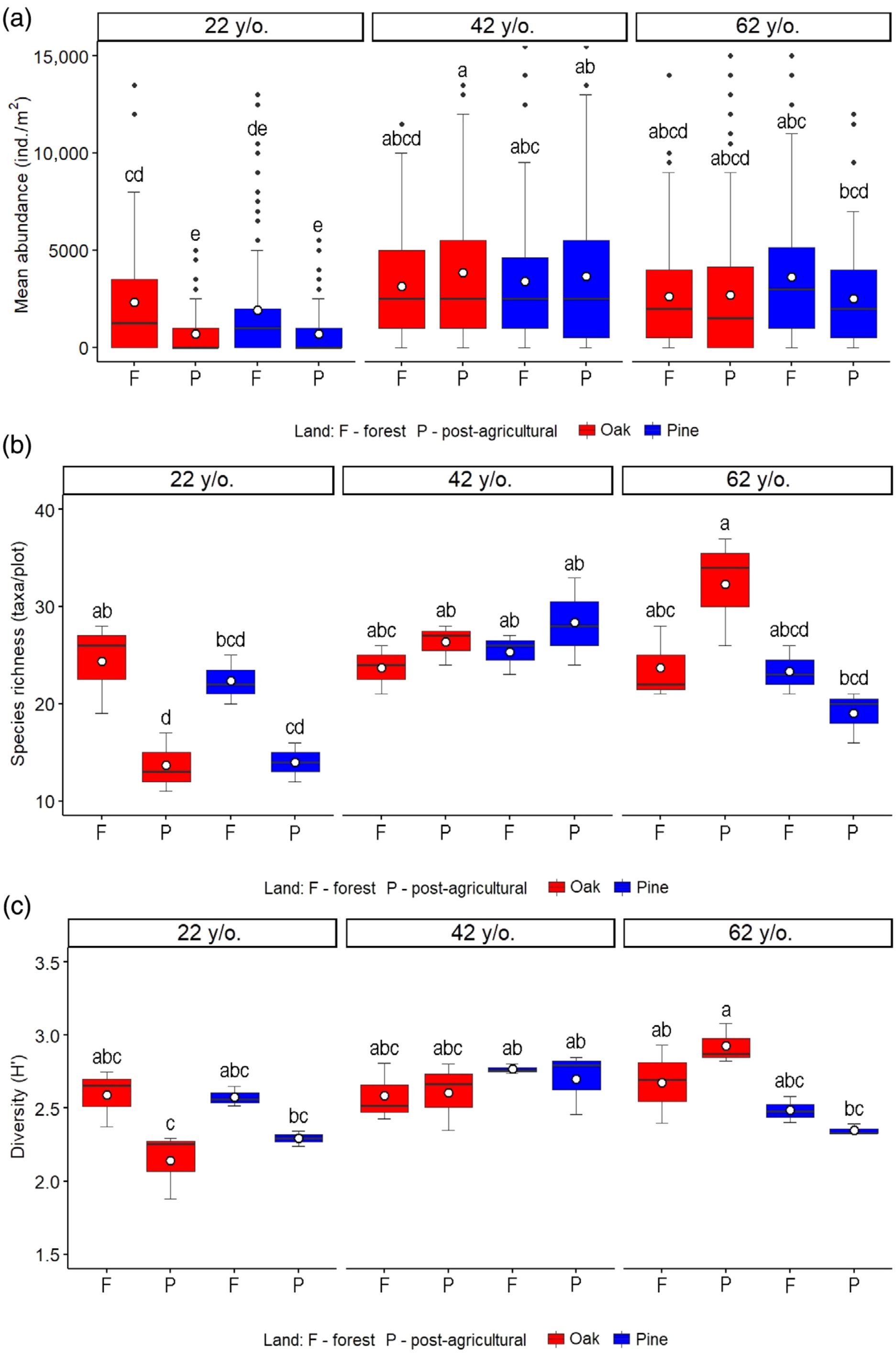

FIGURE 2 Mesostigmatid mite abundance (ind./m^2) (a), species richness (b) and diversity (c) recorded for two tree species between stand age and two examined land use types (data presented as mean values). White dots indicate mean values. [Colour figure can be viewed at wileyonlinelibrary.com]

(2.29 ± 0.03) stands on post-agricultural land (Figure 2c). However, data analysis showed no effect of any soil parameter on diversity. Species richness and diversity increased with each successive stand age only for oak stands growing on post-agricultural land, while in other stands, no such relation was noted. Cumulative species richness conducted for studied habitat types showed a flattering trend of species accrual with increased sampling effort. The curve line for 62 y/o. oak stand, 22 y/o. oak stand and 22 y/o. pine stand growing on post-agricultural land exceeded the curve lines for other examined habitats (Figure 3).

3.3 | Mite communities structure

Most individuals were represented by *Veigaia nemorensis* (C. L. Koch) (985 ind.; 14.64% of all recorded mites), *Zercon peltatus* C. L. Koch (874; 12.99%), *Paragamasus conus* (Karg) (489; 7.27%) and *Rhodacarus coronatus* (Berlese) (481; 7.15%). Thirty-one taxa were classified as rare (<10 ind.). The co-occurrence network for bipartite relationships between mesostigmatid mite taxa and studied habitat types revealed that only eight mesostigmatid mite taxa, that is, *Hypoaspis* (*Gaeolaelaps*) *aculeifer* (Canestrini), *Olodiscus minima* (Kramer), *P. conus*,

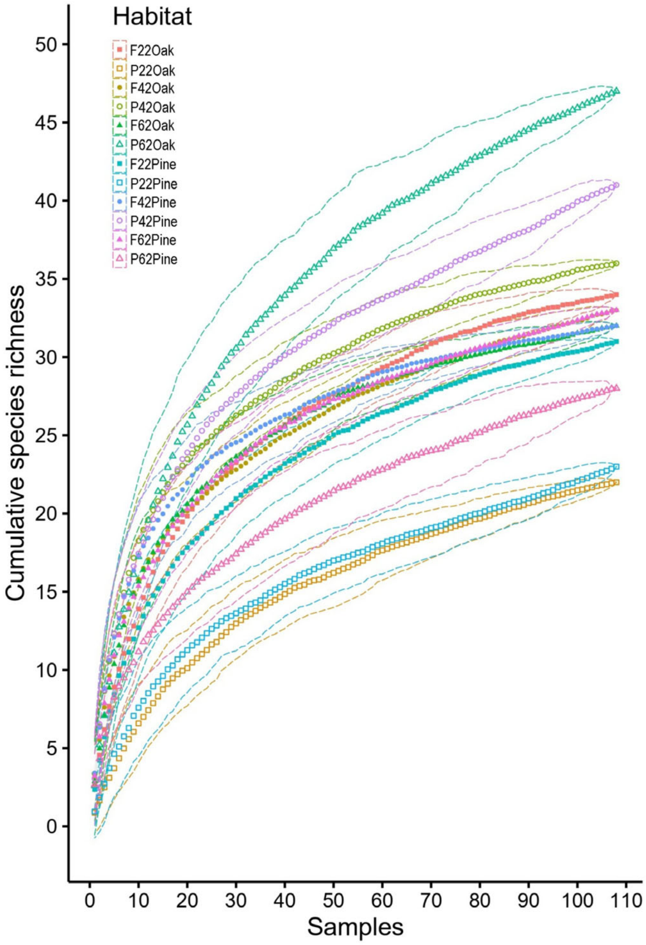

FIGURE 3 Cumulative species richness (data presented as mean values) was recorded for each habitat. 22/42/62 y.o., age of stand; F, forest land; P, post-agricultural land. [Colour figure can be viewed at wileyonlinelibrary.com]

Paragamasus runcatellus, *Paragamasus vagabundus*, *Paragamasus* spp., *Trachytes aegrota* and *V. nemorensis* were recorded from all habitat types studied, whereas 15 mite taxa were unique species for a single habitat type (Figure 4). Except for rare species (<10 ind.), three species were found exclusively on post-agricultural land: *Pachylaelaps longisetis* (Halbert), *Trachytes pauperior* (Berlese) and *Veigaia decurtata* (Athias-Henriot). Further, 12 species (≥10 ind.) were represented more than twice as many on forest land: *Alliphis halleri* (Canestrini & Canestrini), *Anntenoseius bacatus* Athias-Henriot, *Arctoseius venustulus* (Berlese), *Asca aphidioides* (Linnaeus), *Hypoaspis* (*Gaeolaelaps*) *vacua* (Michael), *Lasioseius lawrencei* (Evans), *Leioseius elongatus* (Evans), *Paragamasus jugincola* (Athias-Henriot), *Paragamasus puerilis* (Karg), *Z. peltatus*, *Zercon hungaricus* (Sellnick) and *Zercon triangularis* (C. L. Koch). Analogously, seven species were more abundant on post-agricultural land, compared to forest land: *Laelaspis astronomica* (C. L. Koch), *Oodinychus ovalis* (C. L. Koch), *P. longisetis* (Halbert), *Proctolaelaps juradeus* (Schweizer), *T. pauperior*, *Urodiaspis tecta* (Kramer) and *V. decurtata*. *R. coronatus* was indicated in each stand except the youngest ones on post-agricultural land, and its abundance increased with the age of the stand on forest land, while on post-agricultural land it was highest in a stand of 42 y/o. Similarly, *Rhodacarus mandibularis* Berlese, 1920 and *Z. hungaricus* occurred many times more abundantly in young stands in the forest than in post-agricultural land. In each case, the differences become less clear in older stands.

The CCA revealed significant differences in mite taxa distribution along with constrained components. Axis 1 and 2 explained 38.17% and 29.07% of variance, respectively. Furthermore, analysis of variance conducted for the model showed that soil texture, soil moisture, soil pH and litter K content were significant (Figure 5, Table 2).

4 | DISCUSSION

We revealed that post-agricultural land differs from forest land in terms of the litter thickness, SOM and C/N ratio. These values, were higher on forest land when compared to post-agricultural lands. All the listed parameters are interrelated and their higher values on forest land are typical (Gawęda et al., 2019). As the C/N ratio increases, SOM mineralization decreases (Springob & Kirchmann, 2003). The results indicated that pH of soil has shown significantly higher values on post-agricultural land (Blondeel et al., 2019). Concerning the stand's age, we found differences in litter pH, SOM and C/N ratio. The decrease in soil pH with the age of stands was also confirmed in silver birch (*Betula pendula* Roth), Norway spruce (*P. abies* L.), holm oak (*Q. ilex* L.), downy oak (*Quercus pubescens* Willd) and Allepo pine (*Pinus halepensis* Miller) stands growing on former agricultural land (Cukor et al., 2017; Delcourt et al., 2023; Gawęda et al., 2021). SOM reached the highest value in 42 y/o. stands, which can be explained by the positive impact of thinning, which increases the availability of light in the undergrowth (Gong et al., 2021). Additionally, C/N ratio increased with the age of the forest stands. For instance, Smal et al. (2019) proved that during the first 20–30 years after afforestation of former arable land, the soil has a negligible effect on C_{org} sequestration. Only after about 50 years, the level of C_{org} in post-agricultural soils equals that in forest soils. At the same time, nitrogen content in post-agricultural soil decreases at the beginning of afforestation, after which it begins to increase slowly. However, after 50 years, nitrogen content remains undervalued relative to continuous forest soils.

In general, our study revealed that oak stands had a higher soil pH and litter Ca content than pine stands, which is typical of both tree species and interrelated (Reich et al., 2005). Moreover, Ca content in litter was higher on post-agricultural land than on forest land, suggesting the contribution of past agricultural use to this effect (Olszewska & Smal, 2008), although the results for the soil did not seem to confirm this. In contrast, an interesting result is the highest soil K content in the youngest stands on post-agricultural land, with no variation in this parameter in the litter among stands. Similarly, soil Mn content was highest in the 22 y/o. stands on post-agricultural land. This result contradicts the study of Gawęda et al. (2021), who found that Mn content in topsoil increased with age in naturally regenerated birch stands on abandoned agricultural lands. However,

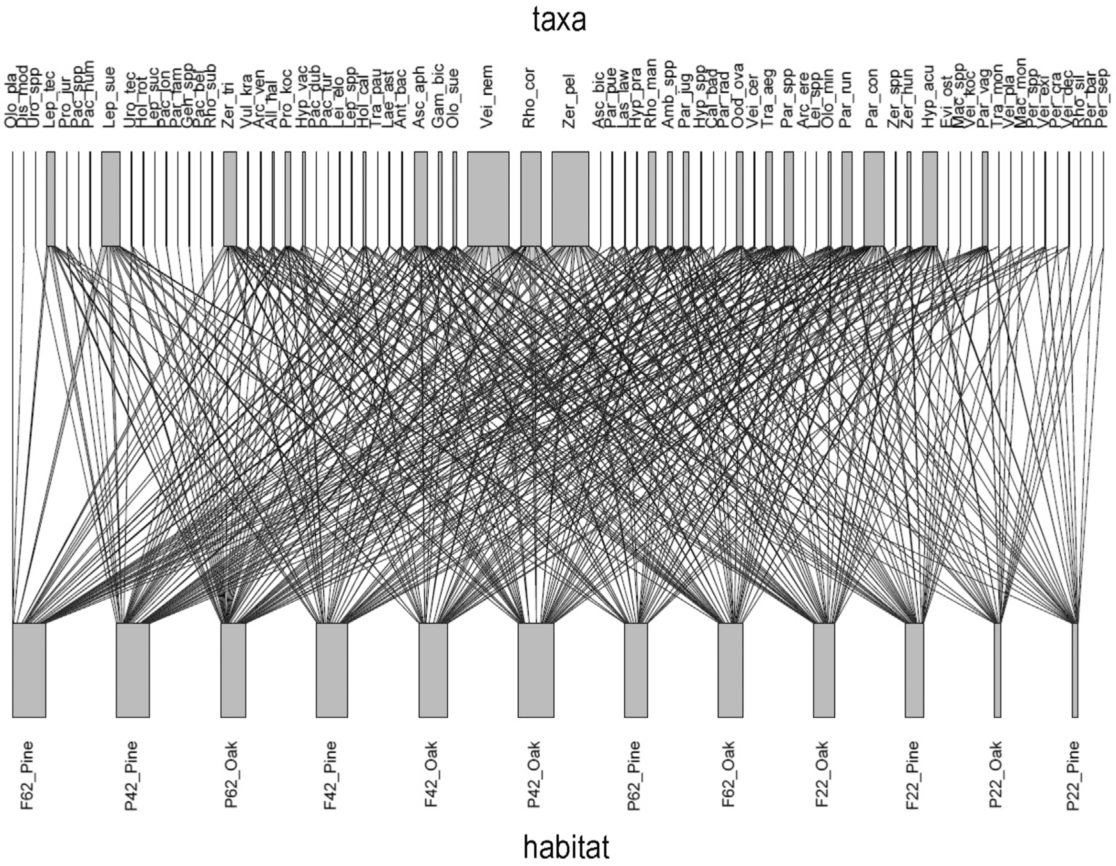

FIGURE 4 Co-occurrence network for bipartite relationships between mesostigmatid mite taxa (upper boxes) and habitat types (lower boxes). Boxes are proportional to total mite abundance, whereas ribbon width is proportional to the proportion of co-occurrence. Abbreviations of mite taxa indicate the first three letters of the genus name and the first three letters of the species name for each mite taxon (for abbreviations of mite taxa see Appendix B). 22/42/62 y/o., age of stand; F, forest land; P, post-agricultural land.

they also recorded the highest soil Ca and K content values in the youngest stands.

Generally, our data revealed that the mite abundance was higher in forest land. However, analysis of individual habitat types shows both the highest and lowest abundance in stands on post-agricultural land. Mite abundance was lower in the youngest oak and pine stands growing on post-agricultural land compared to all other stands. A similar effect of land use history on soil mesofauna abundance was also observed by Harta et al. (2020) and Delcourt et al. (2023). Interestingly, we recorded the highest abundance in 42 y/o. stands on post-agricultural land. The highest abundance in middle age stand can be explained by the positive response of soil fauna to thinning and an increase in light availability in the forest floor (Kamczyc et al., 2021). Furthermore, Delcourt et al. (2023) recorded that after at least 60 years of reforestation, the negative effect of land use legacy on microarthropod communities was no longer observed. The analysis also revealed that mite abundance was influenced by bulk density, litter pH, litter N content and Na and soil Zn content. Our study is partially in line with Bedano et al. (2006), who revealed a positive correlation between soil mite abundance and bulk density and soil pH. In our study, however, this correlation was negative in both cases. Similarly, in contrast to our results, studies of Keshavarz Jamshidian et al. (2015) and Manu et al. (2019) found that soil Zn content affects diversity and species richness but not the abundance of mesostigmatid mites. Additionally, studies carried out by Cao et al. (2011) and Wierzbicka et al. (2019) did not confirm the positive effect of nitrogen on soil mites abundance. However, our previous studies conducted in young stands on post-agricultural land revealed that Na content in forest litter shaped abundance of mesostigmatid mite assemblages (Malica et al., 2024). Also, Ji et al. (2020) proved that a slight increase (0.005%) of Na content in the soil may enhance soil fauna abundance.

Both, the three higher and three lower species richness values were recorded on post-agricultural land. Also, the three lowest values for diversity were found on post-agricultural land. Similar to species richness, diversity was the highest in the oldest and the lowest in the youngest oak stands on post-agricultural land, which was expected. Species richness was the highest in the 62 y/o. oak stand on the post-agricultural land, while it was the lowest in the 22 y/o. oak stand on the post-agricultural land. Doblas-Miranda et al. (2021) proved that oribatid mite density and richness had recovered well on post-agricultural land when it was not isolated from the long-established forest patch (more than 50 years). However, oribatid assemblages in the youngest forests differ from those in long-established stands due to the potential colonization credits and

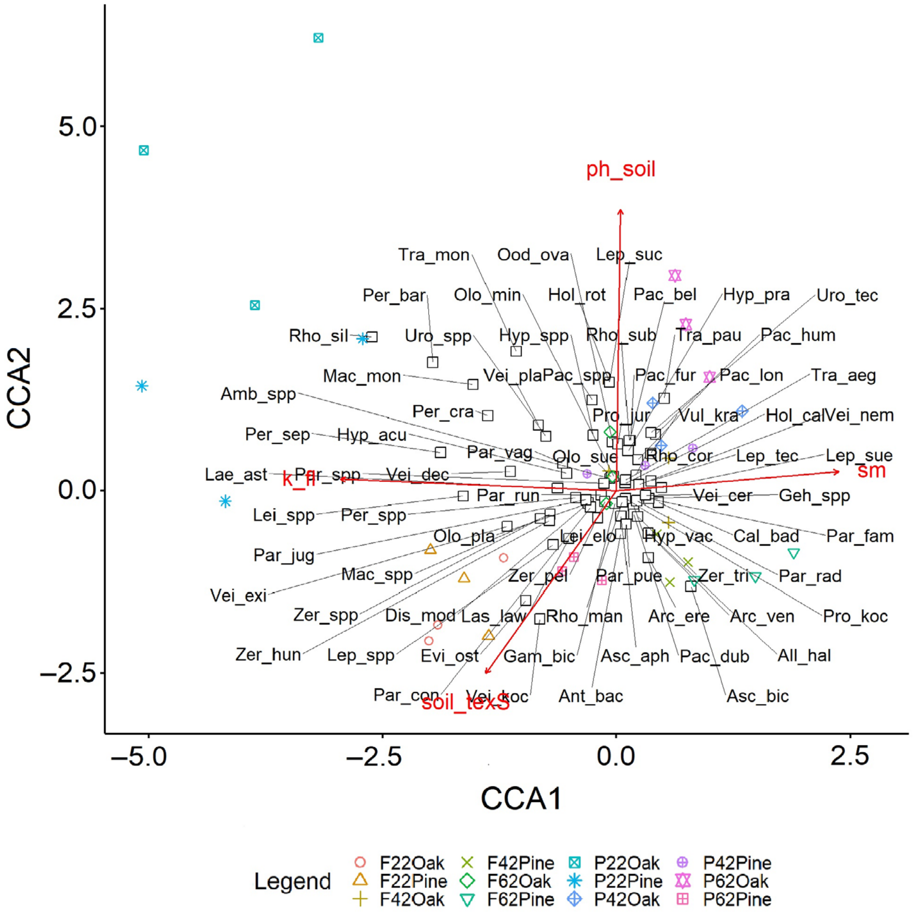

FIGURE 5 Ordination of bi-plot canonical correspondence analysis (CCA) of principal coordinates for Mesostigmata communities occurring in seven habitats. Grey squares show mite taxa labelled with the first three letters of the genus name and the first three letters of the species name for each mite taxon (for abbreviations of mite taxa see Appendix B; see also Table 2 for permutation analysis of variance conducted for final model). 22/42/62, age of stand; F, forest land; k_fl, K content in forest litter; P, post-agricultural land; ph_soil, soil pH; sm, soil moisture; soil_tex, soil texture. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Permutational analysis of variance test of the influence of environmental variables on mite species communities in CCA reduced space.

Predictors	df	Chi square	*F*	Pr(>*F*)
Soil texture	1	0.06077	1.4202	0.086
Soil moisture	1	0.04946	1.1558	0.255
K (litter)	1	0.07907	1.8479	0.013
pH (soil)	1	0.06065	1.4175	0.065
Residual	31	1.32645	AIC	208.48

Abbreviations: AIC, akaike information criterion; k_fl, K content in forest litter; ph_soil, soil pH; sm, soil moisture; soil_tex, soil texture.

extinction debts triggered by soil development. Furthermore, the authors noticed that typical oribatid species dominated in the control stand, occurring in well-developed organic soils, while pioneer species dominated recent forests. We revealed the negative effect of soil Mn content on species richness. This result is consistent with the results of Manu et al. (2017), who studied the impact of heavy metal pollution on mesostigmatid mite communities.

R. coronatus was not recorded in the youngest stands on post-agricultural land. Similarly, *R. mandibularis* and *Z. hungaricus* were more numerous in young stands on forest land. These differences become less explicit in older stands. Given the above, these mite species could be considered potential bioindicators of land use history. However, the use of *R. mandibularis* for this role is questionable since it is a species described in cultivated fields and a pioneer species in post-industrial areas (Skorupski et al., 2013). A similar situation applies to *R. coronatus*, which is considered tolerant of heavy metal contamination in the soil (Seniczak et al., 1997). Mites of Zerconidae family are an important zooedaphon component in all soil microhabitats of the temperate zone. *Z. hungaricus* is xerotolerant and thermophilous species (Manu, 2011). It becomes more important to consider the structure of species, occurring more abundantly on forest land (*A. halleri*, *A. bacatus*, *A. venustulus*, *A. aphidioides* and *H. vacua*, *L. lawrencei*, *L. elongatus*, *P. jugincola*, *P. puerilis*, *Z. peltatus*, *Z. hungaricus* as well as *Z. triangularis*) and those that were more abundant on post-agricultural land (*L. astronomica*, *O. ovalis*, *P. longisetis*, *P. juradeus*, *T. pauperior*, *U. tecta* and *V. decurtata*) as indicator of land use history.

5 | CONCLUSIONS

Our research revealed that soil parameters and mite communities differ primarily between the youngest stands growing on post-agricultural and forest land. We confirmed that these differences disappear with the time passing since afforestation. There are also differences between the effects of pine and oak on the soil environment.

This difference could be explained by the different chemical composition of the leaves (litter), which has an impact on soil proprieties and indirectly on soil Mesostigmata. The highest values of species richness and diversity of mesostigmatid mite communities were recorded in the oldest oak stand on the post-agricultural land, indicating the better influence of this tree species on the soil fauna biodiversity. It is noteworthy that the highest abundance was recorded in middle-aged oak and pine stands on post-agricultural land. This demonstrates that the negative impact of the agricultural history of land use disappears over time. The abundance of mesostigmatid mites also turned out to be more sensitive to differences at the physico-chemical level of the soil than the species richness and diversity of studied mite assemblages. Given insights, They provide a better understanding of land use history on the relations between the soil environment and soil mesostigmatid mites assemblages.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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APPENDIX A: SOIL PROPERTIES OF DIFFERENT HABITAT TYPES

Land	Age	Tree	Soil texture	Litter pH	Litter thick. (cm)	Soil pH	SOM (%)	C_{org} (%)	C/N	BD (g/cm^3)	SM (%)	Soil N (%)	Litter N (%)	Soil Zn (mg/kg)	Litter Zn (mg/kg)
F	22	Oak	Sand	4.47–5.19	2.20–2.50	3.17–3.50	4.24–5.30	2.46–3.08	15.40–20.56	0.68–1.07	7.09–8.22	0.15–0.18	1.40–1.72	5.70–7.21	28.89–30.44
				4.72ab	**2.37gh**	**3.36c**	**4.86a**	**2.82bc**	**17.51abc**	**0.90bcd**	**7.63a**	**0.16bcd**	**1.52bcd**	**6.35bcd**	**29.46ab**
F	22	Pine	Sand	3.73–4.67	3.50–3.80	3.15–4.05	2.55–3.38	1.48–1.96	7.91–13.42	0.65–0.98	3.97–6.79	0.15–0.19	1.43–1.62	4.22–6.78	21.10–27.92
				4.24bcd	**3.60de**	**3.64bc**	**2.86bc**	**1.66de**	**10.55c**	**0.84cd**	**5.28a**	**0.16bcd**	**1.55bc**	**5.11cd**	**25.57bc**
F	42	Oak	Sand	4.98–5.26	4.00–4.50	3.35–3.82	5.66–6.70	3.49–3.96	11.63–12.74	0.61–1.38	4.35–12.27	0.30–0.31	1.76	6.77–7.87	14.64
				5.11a	**4.23d**	**3.61bc**	**6.13a**	**3.72ab**	**12.30abc**	**0.94abcd**	**9.07a**	**0.30a**	**1.76b**	**7.47abc**	**14.64cde**
F	42	Pine	Sand	3.73–5.21	7.00–7.50	3.46–4.12	4.09–6.19	3.55–4.14	14.94–26.03	0.55–1.52	5.00–18.49	0.21–0.27	1.00–2.43	6.73–13.91	12.31–40.33
				3.87de	**7.23a**	**3.55bc**	**5.09a**	**3.85a**	**16.76abc**	**0.66d**	**9.03a**	**0.23abc**	**1.15e**	**10.20ab**	**12.34e**
F	62	Oak	Sand	4.96–5.03	6.00–6.50	3.44–3.80	2.03–2.75	2.18–2.60	8.79–11.81	1.26–1.45	4.45–18.42	0.22–0.26	1.80	4.05–5.10	8.34–10.88
				4.99a	**6.17b**	**3.56bc**	**2.49bc**	**2.44cd**	**10.23c**	**1.37abc**	**10.33a**	**0.24ab**	**1.80b**	**4.48cd**	**9.42e**
F	62	Pine	Sand	3.98–4.01	5.00–5.50	3.47–3.62	2.48–3.39	3.44–4.14	20.37–25.87	1.20–1.52	4.14–12.20	0.13–0.20	1.55	2.70–3.14	14.38–15.66
				3.99cde	**5.27c**	**3.53bc**	**2.99b**	**3.79a**	**23.95a**	**1.35abc**	**8.15a**	**0.16bcd**	**1.55bc**	**2.98cd**	**15.18cde**
P	22	Oak	Sand	4.90–5.43	2.40–2.60	4.29–4.37	1.29–2.35	0.75–1.36	4.40–26.74	1.39–1.46	3.32–4.29	0.05–0.22	1.51–1.88	7.49–14.07	31.35–51.75
				5.18a	**2.47gh**	**4.33a**	**1.93bc**	**1.12e**	**12.29abc**	**1.42ab**	**3.74a**	**0.15bcd**	**1.67b**	**11.57a**	**40.10a**
P	22	Pine	Sand	4.51–4.90	2.90–3.30	3.51–4.02	1.14–1.79	0.66–1.04	5.12–7.28	1.44–1.55	1.27–3.84	0.13–0.15	1.41–1.60	5.74–6.83	22.00–40.01
				4.68abc	**3.03efg**	**3.68bc**	**1.44c**	**0.84e**	**5.97c**	**1.49a**	**2.33a**	**0.14cd**	**1.51bcd**	**6.17bcd**	**31.21ab**
P	42	Oak	Loamy sand	5.01–5.21	2.50–3.10	3.92–4.12	2.23–2.87	1.96–2.43	10.82–11.79	1.05–1.18	12.40–16.20	0.18–0.22	2.21–2.24	2.08–3.10	22.99–30.11
				5.11a	**2.87fg**	**4.01ab**	**2.62bc**	**2.25cd**	**11.18bc**	**1.11abcd**	**13.87a**	**0.20bcd**	**2.23a**	**2.42d**	**25.40bcd**
P	42	Pine	Sand	3.69–4.32	3.50–4.00	3.88–3.90	1.57–1.90	3.35–3.78	15.54–18.88	0.97–1.22	3.67–18.49	0.20–0.22	1.29–1.30	4.91–5.00	34.88–40.33
				3.91de	**3.67de**	**3.89abc**	**1.77bc**	**3.55ab**	**17.05abc**	**1.07abcd**	**9.28a**	**0.21abcd**	**1.29cde**	**4.94cd**	**37.37ab**

(Continues)

Land	Age	Tree	Soil texture	Litter pH	Litter thick. (cm)	Soil pH	SOM (%)	C_{org} (%)	C/N	BD (g/cm^3)	SM (%)	Soil N (%)	Litter N (%)	Soil Zn (mg/kg)	Litter Zn (mg/kg)
P	62	Oak	Loamy sand	4.66–5.01 **4.85ab**	2.00–2.30 **2.10h**	3.70–3.90 **3.83abc**	2.37–2.89 **2.60bc**	2.01–2.23 **2.12cd**	10.09–12.46 **11.26bc**	0.91–1.47 **1.23abc**	4.80–9.53 **6.65a**	0.18–0.21 **0.19bcd**	2.40–2.41 **2.41a**	2.45–2.57 **2.49d**	28.88–29.31 **29.03ab**
P	62	Pine	Sand	3.29–3.44 **3.39e**	3.20–3.50 **3.40ef**	3.21–3.76 **3.54bc**	1.27–2.20 **1.81bc**	2.06–3.28 **2.83bc**	20.86–26.03 **22.95ab**	0.62–1.03 **0.83cd**	6.07–10.06 **8.69a**	0.09–1.15 **0.12d**	1.20–1.22 **1.21de**	1.55–2.13 **1.90d**	12.53 **12.53de**

Land	Age	Tree	Soil texture	Soil Mn (mg/kg)	Litter Mn (mg/kg)	Soil Fe (mg/kg)	Litter Fe (mg/kg)	Soil K (%)	Litter K (%)	Soil Na (%)	Litter Na (%)	Soil Ca (%)	Litter Ca (%)	Soil Mg (%)	Litter Mg (%)
F	22	Oak	Sand	21.13–41.68 **31.31cd**	417.48–431.08 **422.46a**	323.45–368.69 **346.65ab**	126.31–179.10 **159.90c**	0.004–0.006 **0.005ab**	0.052–0.077 **0.067a**	0.002–0.003 **0.002ab**	0.004–0.005 **0.004ab**	0.003–0.004 **0.003b**	0.167–0.186 **0.175cd**	0.175–0.182 **0.179b**	0.200–0.206 **0.203ab**
F	22	Pine	Sand	48.84–68.80 **60.50c**	336.12–411.22 **383.13a**	335.87–359.42 **351.53ab**	69.84–96.29 **86.75d**	0.004–005 **0.004ab**	0.037–0.046 **0.041a**	0.002–0.003 **0.002ab**	0.004–0.006 **0.005a**	0.001–0.005 **0.003b**	0.131–168 **0.155cd**	0.179–0.183 **0.181ab**	0.195–0.202 **0.199b**
F	42	Oak	Sand	1.10–3.56 **2.58d**	122.10–122.65 **122.46d**	209.62–215.44 **211.56b**	86.44–90.89 **87.92d**	0.002–0.003 **0.002b**	0.010–0.011 **0.011a**	0.002 **0.002ab**	0.001–0.003 **0.003b**	0.003–0.005 **0.004b**	0.227–0.228 **0.227bc**	0.005 **0.005c**	0.021–0.032 **0.029de**
F	42	Pine	Sand	1.64–68.80 **2.30d**	76.65–431.08 **76.65de**	175.88–470.54 **260.45b**	219.25–235.90 **220.27ab**	0.002–0.006 **0.003ab**	0.009–0.132 **0.009a**	0.002–0.003 **0.003a**	0.003–0.006 **0.004ab**	0.010–0.022 **0.016a**	0.068–0.440 **0.073d**	0.005–0.183 **0.006c**	0.011–0.206 **0.012f**
F	62	Oak	Sand	4.10–5.90 **5.03d**	239.08–273.08 **261.38b**	299.60–299.61 **299.61ab**	70.77–72.00 **71.41d**	0.002 **0.002b**	0.010–0.132 **0.052a**	0.002 **0.002ab**	0.003 **0.003b**	0.005 **0.005b**	0.128–0.138 **0.135cd**	0.007 **0.007c**	0.035–0.039 **0.037cd**
F	62	Pine	Sand	2.46–11.17 **8.19d**	209.88–217.24 **214.70bc**	192.83–332.08 **275.01b**	100.98–102.30 **101.68d**	0.001–0.002 **0.001b**	0.012–0.013 **0.013a**	0.001–0.002 **0.002b**	0.003 **0.003b**	0.001–0.004 **0.003b**	0.119–0.122 **0.120cd**	0.003–0.005 **0.004c**	0.021 **0.021ef**
P	22	Oak	Sand	295.83–359.36 **326.68a**	420.93–434.67 **427.34a**	331.42–343.85 **338.34ab**	184.37–253.80 **219.26ab**	0.006–0.009 **0.008a**	0.065–0.800 **0.073a**	0.002–0.003 **0.003a**	0.003–0.005 **0.004ab**	0.000–0.004 **0.002b**	0.185–0.188 **0.187cd**	0.184–0.187 **0.186a**	0.208–0.211 **0.209a**
P	22	Pine	Sand	106.77–155.42 **135.40b**	395.76–427.06 **415.70a**	331.93–438.07 **342.11ab**	163.26–181.90 **174.74c**	0.004–0.015 **0.008a**	0.050–0.060 **0.057a**	0.002 **0.002ab**	0.003 **0.004ab**	0.001 **0.003b**	0.167 **0.176cd**	0.183 **0.185a**	0.202 **0.202ab**

Land	Age	Tree	Soil texture	Soil Mn (mg/kg)	Litter Mn (mg/kg)	Soil Fe (mg/kg)	Litter Fe (mg/kg)	Soil K (%)	Litter K (%)	Soil Na (%)	Litter Na (%)	Soil Ca (%)	Litter Ca (%)	Soil Mg (%)	Litter Mg (%)
P	42	Oak	Loamy sand	3.99–4.09	190.47–235.09	300.56–402.89	89.03–90.09	0.002	0.017–0.019	0.002	0.002–0.003	0.003	0.280–0.425	0.005–0.009	0.030–0.039
				4.04d	**220.00bc**	**347.84ab**	**89.72d**	**0.002b**	**0.018a**	**0.002b**	**0.003b**	**0.003b**	**0.345ab**	**0.007c**	**0.036cd**
P	42	Pine	Sand	2.01–3.91	175.75–180-65	300.01–340-77	220.41–235.90	0.001	0.021–0.022	0.002	0.004–0.005	0.001–0.003	0.110–0.340	0.004–0.007	0.035–0.037
				2.68d	**177.78c**	**320.58ab**	**230.38a**	**0.001b**	**0.022a**	**0.002ab**	**0.005ab**	**0.002b**	**0.220bc**	**0.005c**	**0.036cd**
P	62	Oak	Loamy sand	5.10–6.98	369.10–400.10	400.22	89.09	0.002	0.017	0.002	0.002–0.003	0.001–0.003	0.344–0.440	0.004	0.043–0.045
				6.35d	**381.15a**	**446.45a**	**89.77d**	**0.002b**	**0.017a**	**0.002b**	**0.002b**	**0.001b**	**0.380a**	**0.004c**	**0.043c**
P	62	Pine	Sand	1.69–0.197	40.78–50.77	187.48–237.28	160.76–187.09	0.001	0.007–0.077	0.002	0.003–0.004	0.001–0.005	0.079–0.096	0.003–0.005	0.013–0.014
				1.79d	**44.36e**	**219.58b**	**176.86bc**	**0.001b**	**0.030a**	**0.002ab**	**0.003ab**	**0.003b**	**0.088d**	**0.004c**	**0.014f**

Note: Bold values with different letters indicate significant differences between habitats (in columns).

Abbreviations: BD, bulk density; C_{org}, organic carbon content; F, forest land; Litter thick., litter thickness; P, post-agricultural land; SM, soil moisture; SOM, soil organic matter.

APPENDIX B: NETWORK STATISTICS FOR MESOSTIGMATID MITE TAXA, DESCRIBING THEIR AFFILIATION TO STUDIED HABITATS AND SPECIALIZATION

Mite taxa	Mite taxa abbreviation	Number of habitats	Proportion of habitats	Species specifity index *d'*
Alliphis halleri (Canestrini & Canestrini, 1881)	All_hal	8	0.67	0.40
Amblyseius spp. (Berlese, 1904)	Amb_spp	10	0.83	0.26
Antennoseius bacatus Athias-Henriot, 1961	Ant_bac	8	0.67	0.34
Arctoseius eremitus (Berlese, 1918)	Arc_ere	1	0.08	1.00
Arctoseius venustulus (Berlese, 1917)	Arc_ven	8	0.67	0.40
Asca aphidioides (Linnaeus, 1758)	Asc_aph	11	0.92	0.21
Asca bicornis (Canestrini & Fanzago, 1887)	Asc_bic	1	0.08	1.00
Calaenopsis badius (C. L. Koch, 1839)	Cal_bad	3	0.25	0.64
Discourella modesta (Leonardi, 1889)	Dis_mod	1	0.08	1.00
Eviphis ostrinus (C. L. Koch, 1836)	Evi_ost	2	0.17	0.72
Gamasellodes bicolor (Berlese, 1918)	Gam_bic	11	0.92	0.27
Geholaspis spp. (Berlese, 1918)	Geh_spp	1	0.08	1.00
Holoparasitus calcaratus (C. L. Koch, 1839)	Hol_cal	8	0.67	0.37
Holoparasitus rotulifer (Willmann, 1940)	Hol_rot	1	0.08	1.00
Hypoaspis (*Gaeolaelaps*) *aculeifer* (Canestrini, 1883)	Hyp_acu	12	1.00	0.15
Hypoaspis (*Gaeolaelaps*) spp. (Canestrini, 1884)	Hyp_spp	9	0.75	0.31
Hypoaspis (*Gaeolaelaps*) *vacua* (Michael, 1891)	Hyp_vac	6	0.50	0.80
Hypoaspis (*Gaeolaelaps*) *praesternalis* (Willmann, 1949)	Hyp_pra	5	0.42	0.43
Laelaspis astronomica (C. L. Koch, 1839)	Lae_ast	4	0.33	0.62
Lasioseius lawrencei (Evans, 1958)	Las_law	6	0.50	0.44
Leioseius elongatus Evans, 1958	Lei_elo	6	0.50	0.45
Leioseius spp. (Berlese, 1916)	Lei_spp	1	0.08	1.00
Leptogamasus spp. (Trägårdh, 1936)	Lep_spp	2	0.17	0.67
Leptogamasus succineus Witaliński, 1973	Lep_suc	1	0.08	1.00
Leptogamasus suecicus (Trägårdh, 1936)	Lep_sue	8	0.67	0.31
Leptogamasus tectegynellus (Athias Henriot, 1967)	Lep_tec	7	0.58	0.44
Macrocheles montanus (Willmann, 1951)	Mac_mon	3	0.25	0.62
Macrocheles spp. (Latreille, 1829)	Mac_spp	2	0.17	0.67
Olodiscus minima (Kramer, 1882)	Olo_min	12	1.00	0.25
Ololaelaps placentula (Berlese, 1887)	Olo_pla	1	0.08	1.00
Olopachys suecicus (Sellnick, 1950)	Olo_sue	8	0.67	0.27
Oodinychus ovalis (C. L. Koch, 1839)	Ood_ova	10	0.83	0.35
Pachylaelaps bellicosus (Berlese, 1920)	Pac_bel	1	0.08	1.00
Pachylaelaps dubius (Hirschmann & Krauss, 1965)	Pac_dub	2	0.17	0.72
Pachylaelaps furcifer (Oudemans, 1903)	Pac_fur	2	0.17	0.72
Pachylaelaps longisetis (Halbert, 1915)	Pac_lon	1	0.08	1.00
Pachylaelaps spp. (Berlese, 1886)	Pac_spp	2	0.17	0.72
Pachyseius humeralis (Berlese, 1910)	Pac_hum	2	0.17	0.77
Paragamasus conus (Karg, 1971)	Pac_con	12	1.00	0.18
Paragamasus jugincola (Athias Henriot, 1967)	Par_jug	10	0.83	0.24
Paragamasus puerilis (Karg, 1963)	Par_pue	6	0.50	0.37
Paragamasus runcatellus (Berlese, 1903 sensu Karg, 1971)	Par_run	12	1.00	0.27

Mite taxa	Mite taxa abbreviation	Number of habitats	Proportion of habitats	Species specifity index d'
Paragamasus spp. (Hull, 1918)	Par_spp	12	1.00	0.14
Paragamasus vagabundus (Karg, 1968)	Par_vag	12	1.00	0.24
Parasitidae	Par_fam	1	0.08	1.00
Parazercon radiatus (Berlese, 1914)	Par_rad	2	0.17	0.67
Pergamasus barbarus (Berlese, 1904)	Per_bar	2	0.17	0.67
Pergamasus crassipes (Linnaeus, 1758)	Per_cra	3	0.25	0.56
Pergamasus septentrionalis (Oudemans, 1902)	Per_sep	2	0.17	0.72
Pergamasus spp. (Berlese, 1903)	Per_spp	2	0.17	0.67
Proctolaelaps juradeus (Schweizer, 1949)	Pro_jur	3	0.25	0.59
Prozercon kochi (Sellnick, 1943)	Pro_koc	10	0.83	0.26
Rhodacarellus silesiacus (Willmann, 1936)	Rho_sil	1	0.08	1.00
Rhodacarellus subterraneus (Willmann, 1935)	Rho_sub	1	0.08	1.00
Rhodacarus coronatus (Berlese, 1921)	Rho_cor	10	0.83	0.33
Rhodacarus mandibularis (Berlese, 1921)	Rho_man	10	0.83	0.29
Trachytes aegrota (C. L. Koch, 1841)	Tra_aeg	12	1.00	0.16
Trachytes montana Willmann, 1953	Tra_mon	2	0.17	0.67
Trachytes pauperior (Berlese, 1914)	Tra_pau	3	0.25	0.61
Urodiaspis tecta (Kramer, 1876)	Uro_tec	4	0.33	0.51
Uropoda spp. (Latreille, 1806)	Uro_spp	1	0.08	1.00
Veigaia cerva (Kramer, 1876)	Vei_cer	8	0.67	0.26
Veigaia decurtata (Athias Henriot, 1961)	Vei_dec	4	0.33	0.60
Veigaia exigua (Berlese, 1916)	Vei_exi	6	0.50	0.54
Veigaia kochi (Trägårdh, 1901)	Vei_koc	1	0.08	1.00
Veigaia nemorensis (C. L. Koch, 1839)	Vei_nem	12	1.00	0.20
Veigaia planicola (Berlese, 1892)	Vei_pla	5	0.42	0.43
Vulgarogamasus kraepelini (Berlese, 1904)	Vul-Kra	6	0.50	0.45
Zercon peltatus (C. L. Koch, 1836)	Zer_pel	11	0.92	0.19
Zercon hungaricus (Sellnick, 1958)	Zer_hun	7	0.58	0.47
Zercon spp. (C. L. Koch, 1836)	Zer_spp	2	0.17	0.72
Zercon triangularis (C. L. Koch, 1836)	Zer_tri	10	0.83	0.37

APPENDIX C: TUKEY POSTERIORI TEST FOR SOIL PROPERTIES AMONG STUDIED HABITATS

	Soil properties																					
Terms	Litter pH	Litter thick.	Soil pH	SOM	C_{org}	C/ N	BD	Soil N	Litter N	Soil Zn	Litter Zn	Soil Mn	Litter Mn	Soil Fe	Litter Fe	Soil K	Soil Na	Litter Na	Soil Ca	Litter Ca	Soil Mg	Litter Mg
F22Oak–F22Pine	-	***	-	**	**	-	-	-	-	-	-	-	-	-	***	-	-	-	-	-	-	-
F22Oak–F42Oak	-	***	-	-	-	-	-	**	-	-	*	-	***	-	***	-	-	-	-	-	***	***
F22Oak–F42Pine	*	***	-	-	*	-	-	-	*	-	**	-	***	-	**	-	-	-	***	-	***	***
F22Oak–F62Oak		***	-	***	-	-	-	-	-	-	***	-	***	-	***	-	-	-	-	-	***	***
F22Oak–F62Pine	*	***	-	**	*	-	-	-	-	-	*	-	***	-	**	-	-	-	-	-	***	***
F22Oak–P22Oak	-	-	***	***	***	-	-	-	-	*	-	***	-	-	**	-	-	-	-	-	**	-
F22Oak–P22Pine	-	-	-	***	***	-	*	-	-	-	-	***	-	-	-	-	-	-	-	-	**	-
F22Oak–P42Oak	-	-	*	***	-	-	-	-	***	-	-	-	***	-	***	-	-	-	-	**	***	***
F22Oak–P42Pine	*	***	-	***	-	-	-	-	-	-	-	-	***	-	***	-	-	-	-	-	***	***
F22Oak–P62Oak	-	-	-	***	-	-	-	-	***	-	-	-	-	-	***	-	-	-	-	***	***	***
F22Oak–P62Pine	***	***	-	***	-	-	-	-	-	-	**	-	***	-	-	-	-	-	-	-	***	***
F22Pine–F42Oak	**	-	-	***	***	-	-	***	-	-	-	***	***	-	-	-	-	**	-	-	***	***
F22Pine–F42Pine	-	***	-	***	***	-	-	-	**	*	*	***	***	-	***	-	-	-	***	-	***	***
F22Pine–F62Oak	*	***	-	-	-	-	-	-	-	-	**	***	***	-	-	-	-	**	-	-	***	***
F22Pine–F62Pine	-	***	-	-	***	*	-	-	-	-	-	**	***	-	-	-	-	**	-	-	***	***
F22Pine–P22Oak	**	***	*	-	-	-	*	-	-	**	*	***	-	-	***	-	-	-	-	-	-	*
F22Pine–P22Pine	-	-	-	-	-	-	*	-	-	-	-	***	-	-	***	-	-	-	-	-	-	-
F22Pine–P42Oak	**	*	-	-	-	-	-	-	***	-	-	***	***	-	-	-	-	**	-	***	***	***
F22Pine–P42Pine	-	-	-	-	***	-	-	-	-	-	-	***	***	-	***	-	-	-	-	-	***	***
F22Pine–P62Oak	-	***	-	-	-	-	-	-	***	-	-	***	-	-	-	-	-	**	-	***	***	***
F22Pine–P62Pine	*	-	-	-	**	*	-	-	*	-	*	***	***	-	***	-	-	-	-	-	***	***
F42Oak–F42Pine	***	***	-	-	-	-	-	-	***	-	-	-	-	-	***	-	-	-	***	**		***
F42Oak–F62Oak	-	***	-	***	**	-	-	-	-	-	-	-	***	-	-	-	-	-	-	-	-	-
F42Oak–F62Pine	***	***	-	***	-	-	-	**	-	-	-	-	***	-	-	-	-	-	-	-	-	-
F42Oak–P22Oak	-	***	*	***	***	-	-	***	-	-	***	***	***	-	***	*	-	-	-	-	***	***
F42Oak–P22Pine	-	***	-	***	***	-	-	***	-	-	**	***	***	-	***	*	-	-	-	-	***	***
F42Oak–P42Oak	-	***	-	***	***	-	-	*	**	*	-	-	***	-	-	-	-	-	-	-	-	-
F42Oak–P42Pine	***	-	-	***	-	-	-	-	**	-	***	-	*	-	***	-	-	-	-	-	-	-
F42Oak–P62Oak	-	***	-	***	***	-	-	*	***	*	*	-	***	***	-	-	-	-	-	**	-	***
F42Oak–P62Pine	***	**	-	***	-	-	-	***	***	**	-	-	***	-	***	-	-	-	-	*	-	***

	Soil properties																					
Terms	Litter pH	Litter thick.	Soil pH	SOM	C_{org}	C/N	BD	Soil N	Litter N	Soil Zn	Litter Zn	Soil Mn	Litter Mn	Soil Fe	Litter Fe	Soil K	Soil Na	Litter Na	Soil Ca	Litter Ca	Soil Mg	Litter Mg
F42Pine–F62Oak	***	***	-	***	***	-	**	-	***	**	-	-	***	-	***	-	-	-	***	-	-	***
F42Pine–F62Pine	-	***	-	**	-	-	**	-	**	***	-	-	***	-	***	-	**	-	***	-	-	-
F42Pine–P22Oak	***	***	**	***	***	-	**	-	***	-	***	***	***	-	-	-	-	-	***	-	***	***
F42Pine–P22Pine	*	***	-	***	***	-	***	-	*	-	**	***	***	-	*	-	-	-	***	-	***	***
F42Pine–P42Oak	***	***	-	***	***	-	-	-	***	***	*	-	***	-	***	-	*	-	***	***	-	***
F42Pine–P42Pine	-	***	-	***	-	-	-	-	-	*	***	-	***	-	-	-	-	-	***	*	-	***
F42Pine–P62Oak	**	***	-	***	***	-	*	-	***	***	**	-	***	**	***	-	*	-	***	***	-	***
F42Pine–P62Pine	-	***	-	***	*	-	-	*	-	***	-	-	-	-	-	-	-	-	***	-	-	-
F62Oak–F62Pine	**	**	-	-	**	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	***
F62Oak–P22Oak	-	***	**	-	**	-	-	-	-	***	***	***	***	-	***	*	-	-	-	-	***	***
F62Oak–P22Pine	-	***	-	-	***	-	-	*	-	-	***	***	***	-	***	*	-	-	-	-	***	***
F62Oak–P42Oak	-	***	-	-	-	-	-	-	**	-	**	-	-	-	-	-	-	-	-	***	-	-
F62Oak–P42Pine	***	***	-	-	**	-	-	-	***	-	***	-	***	-	***	-	-	-	-	-	-	-
F62Oak–P62Oak	-	***	-	-	-	-	-	-	***	-	***	-	***	-	-	-	-	-	-	***	-	-
F62Oak–P62Pine	***	***	-	-	-	*	-	**	***	-	-	-	***	-	***	-	-	-	-	-	-	***
F62Pine–P22Oak	***	***	**	-	***	-	-	-	-	***	***	***	***	-	***	*	**	-	-	-	***	***
F62Pine–P22Pine	-	***	-	*	***	***	-	-	-	-	**	***	***	-	***	**	-	-	-	-	***	***
F62Pine–P42Oak	***	***	-	-	***	*	-	-	***	-	-	-	-	-	-	-	-	-	-	***	-	***
F62Pine–P42Pine	-	***	-	-	-	-	-	-	-	-	***	-	-	-	***	-	-	-	-	-	-	***
F62Pine–P62Oak	**	***	-	-	***	*	-	-	***	-	*	-	***	*	-	-	-	-	-	***	-	***
F62Pine–P62Pine	-	***	-	-	*	-	-	-	*	-	-	-	***	-	***	-	-	-	-	-	-	-
P22Oak–P22Pine	-	-	*	-	-	-	-	-	-	*	-	***	-	-	*	-	-	-	-	-	-	-
P22Oak–P42Oak	-	-	-	-	**	-	-	-	***	***	*	***	***	-	***	*	*	-	-	**	***	***
P22Oak–P42Pine	***	***	-	-	***	-	-	-	*	**	-	***	***	-	-	*	-	-	-	-	***	***
P22Oak–P62Oak	-	-	-	-	*	-	-	-	***	***	-	***	-	-	***	*	*	-	-	***	***	***
P22Oak–P62Pine	***	**	**	-	***	-	*	-	**	***	***	***	***	-	-	**	-	-	-	-	***	***
P22Pine–P42Oak	-	-	-	-	***	-	-	-	***	-	-	***	***	-	***	*	-	-	-	**	***	***
P22Pine–P42Pine	*		-	-	***	-	-	-	-	-	-	***	***	-	**	**	-	-	-	-	***	***
P22Pine–P62Oak	-	**	-	-	**	-	-	-	***	-	-	***	-	-	***	*	-	-	-	***	***	***
P22Pine–P62Pine	***	-	-	-	***	**	*	-	-	-	**	***	***	-	-	**	-	-	-	-	***	***
P42Oak–P42Pine	***	*	-	-	**	-	-	-	***	-	-	-	-	-	***		-	-	-	-	-	-
P42Oak–P62Oak	-	*	-	-	-	-	-	-	-	-	-	-	***	-	-	-	-	-	-	-	-	-

(Continues)

Terms	Soil properties																					
	Litter pH	Litter thick.	Soil pH	SOM	C_{org}	C/N	BD	Soil N	Litter N	Soil Zn	Litter Zn	Soil Mn	Litter Mn	Soil Fe	Litter Fe	Soil K	Soil Na	Litter Na	Soil Ca	Litter Ca	Soil Mg	Litter Mg
P42Oak–P62Pine	***	-	-	-	-	-	-	-	***	-	-	-	***	-	***	-	-	-	-	***	-	***
P42Pine–P62Oak	**	***	-	-	***	-	-	-	***	-	-	-	***	-	***	-	-	-	-	**	-	-
P42Pine–P62Pine	-	-	-	-	-	-	-	-	-	-	***	-	***	-	**	-	-	-	-	*	-	***
P62Oak–P62Pine	***	***	-	-	-	-	-	-	***	-	**	-	***	***	***	-	-	-	-	***	-	***
F62Oak–F62Pine	**	**	-	-	**	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	***
F62Oak–P22Oak	-	***	**	-	**	-	-	-	-	***	***	***	***	-	***	*	-	-	-	-	***	***
F62Oak–P22Pine	-	***	-	-	***	-	-	*	-	-	***	***	***	-	***	*	-	-	-	-	***	***
F62Oak–P42Oak	-	***	-	-	-	-	-	-	**	-	**	-	-	-	-	-	-	-	-	***	-	-
F62Oak–P42Pine	***	***	-	-	**	-	-	-	***	-	***	-	***	-	***		-	-	-	-	-	-

Abbreviations: 22/42/62, age of stand; F, forest land; P, post-agricultural land.
Signif. codes: *p Value ≤ 0.05; **p Value ≤ 0.01; *p Value ≤ 0.

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RESEARCH

Soil mite communities (Acari, Mesostigmata) in pure stands on post-agricultural lands: does season matter?

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Abstract

Post-agricultural land differs from typical forest land in physical, chemical and biological features. In addition, the environment of this land type is determined, among other things, by the introduced tree species. These differences may be revealed by the biodiversity and abundance of the soil fauna. We analysed the abundance, species richness and diversity of different instars of mesostigmatid mites inhabiting three different habitat types on post-agricultural land (shaped by pure *Pinus sylvestris* L., *Tilia cordata* Mill. and *Betula pendula* Roth stands). We collected 288 soil samples from eight plots in three stands. The collection was conducted in July and October in two consecutive vegetation seasons (2021 and 2022) for Mesostigmata mites community. Soil characteristics (determination of soil group and analysis of physical and chemical properties of soil and litter) were done in July 2021. In total, 399 individuals (266 females, 50 males and 83 juveniles) were classified into 38 taxa (33 species, five genera). Most individuals belonged to the Parasitidae, Laelapidae and Veigaiidae families. The most abundant species were *Hypoaspis aculeifer* (Canestini) (21.6% of all recorded mites), *Veigaia nemorensis* (C.L.Koch) (7.8%) and *Trachytes aegrota* (C.L.Koch) (7.0%). Abundance, species richness and diversity were shaped by collection month and Fe content in soil. The abundance was influenced by N litter content and was significantly lower in *P. sylvestris* stand in July (0.57 ± 0.23; mean ± SE) than in *P. sylvestris* (2.17 ± 0.54) and *T. cordata* (2.15 ± 0.48) stands in October. Moreover, abundance in *P. sylvestris* stand in October was higher than in *B. pendula* stand in July (0.78 ± 0.26). Similarly, species richness was significantly lower in *P. sylvestris* stand in July than in *P. sylvestris* and *T. cordata* stands in October (2.17 ± 0.54 and 2.15 ± 0.48, respectively). Higher Shannon's diversity of mite communities was reported in *P. sylvestris* stand in October (0.40 ± 0.10) than in *P. sylvestris* and *B. pendula* stands in July (0.12 ± 0.06 and 0.14 ± 0.08, respectively). Large fluctuations of abundance, species richness and diversity of soil mite communities in *P. sylvestris* and *B. pendula* stands between collection months give the insights for creating mixed stands on post-agricultural land. It is worth noticing that the wet season creates the most favourable living environment for mesostigmatid mites in *P. sylvestris* litter.

Extended author information available on the last page of the article

Keywords Afforestation · Forest biodiversity · Post-agricultural land · Soil fauna · Mesostigmata

Introduction

The area of forests in Poland increased between 1945 and 2012 from 21 to 30% (i.e. from 6,470,000 ha to 9,164,000 ha). Such growth occurred primarily through the afforestation of post-agricultural lands (Kaliszewski 2016), accounting for 55% of afforestation—1,477,000 ha (Krawczyk 2015). Afforested post-agricultural land differs in physical and chemical characteristics from typical forest land. The most important differences include a higher pH and a lower C:N ratio. This results from long-term agricultural use—repeated ploughing and fertilization. Ploughing is responsible for the transformation of the soil profile and fertilization for the chemical changes (Gorzelak 1996). Additional differences are generated by the fact that these lands have been deprived for many years of the influence of tree root systems, which stabilize the soil structure and enrich it biologically (Thoms et al. 2010). The greater biodiversity of bacteria and lower diversity of fungi in soils of post-agricultural lands may be triggered by higher availability of nutrients (Delgado-Baquerizo et al. 2017). Planting of trees on post-agricultural land shapes the succession process of herbaceous plants and shrubs. This process is long-lasting and depends on the fragmentation of habitats and the vicinity of inhabited stands (Ciurzycki et al. 2021). The diversity of different plant functional groups may be positively correlated with soil functions such as microbial biomass carbon, basal respiration, and carbon sequestration. Thus, with the ongoing succession of these groups on post-agricultural land, the parameters may improve (Heydari et al. 2020). Both land use history and soil type are, therefore, a set of abiotic factors that shape the living conditions of trees and soil organisms. The importance of soil biota in soil remediation processes is based on their contribution to the decomposition of dead organic matter. Fungi, bacteria, nematodes (Nematoda), springtails (Collembola) and soil mites (Acari) should be considered as the main groups of such organisms. Good bioindicators of changes in the soil environment are free-living mesostigmatid mites (Mesostigmata). They occur in large numbers in the soil and forest litter, lead a relatively sedentary lifestyle (Kamczyc et al. 2019) and are sensitive to pollution and degradation of forest areas (Manu et al. 2019). They hunt primarily on springtails, nematodes, potworms (Enchytraeidae) or insect larvae (Insecta) (Koehler 1999; Wissuwa et al. 2012). The structure of mesostigmatid mite communities depends on the particular conditions of habitat type, such as vegetation, age of the trees or human impact and abiotic factors. Mesostigmatid mites highlight the degree of anthropogenization in ecosystems, but this effect is especially pronounced in forests (Călugăr, 2021). Mesostigmatid mite communities are also subject to seasonal changes in species composition and abundance concerning temperature and precipitation (Salmane 2000; Kamczyc et al. 2022). Environmental conditions and seasonal dynamics are also expressed through changes in the relationships of different mesostigmatid developmental instars, which include adult (males, females) and three juvenile instars (deutonymphs, protonymphs and larvae) (Urbanowski et al. 2021).

The aim of the study was to recognize differences in seasonal changes in the abundance, species richness and diversity of Mesostigmata mite assemblages inhabiting pure forests (*Betula pendula* Roth, *Tilia cordata* Mill., *Pinus sylvestris* L.) growing on post-agricultural lands. Considering previous studies on post-agricultural lands (Scheu and Schulz 1996; Gormsen et al. 2006; Gawęda et al. 2021), we hypothesized that abundance, species richness, diversity, and relative proportion of different instars (including sex ratio) in mite communities would respond in different ways to (1) season (summer and autumn), (2) tree species, and (3) soil properties. We expected that various forest litter types would affect soil mite assemblages differently, and that effect would change with season.

Materials and methods

Site description and experimental design

The study site was located in the Opole Forest District (S–W Poland), where coniferous forests cover 60% of the forest area. The forests are dominated by mesic (57% of area), moist (40%), and marsh sites (~3%). Considering the soil environment, the main groups of soils are Arenosols (rusty soils)—45.3%, Podzols (podzolic soils)—23.0%, and Gleysols (gleyic soils)—16.4% (Forest Management Plan for Opole Forest Division, 2014). The vegetation season lasts 227 days. Mean annual precipitation reaches 603 mm, while mean annual temperature is 8 °C. The duration of winter is 60–70 days, and the number of days with snow cover is 58–65 days. In turn, the duration of summer is 90–100 days (Malica et al. 2024).

At the beginning of our study, three pure stands of different tree species (*Pinus sylvestris* L., *Tilia cordata* Mill. and *Betula pendula* Roth) were selected (Fig. 1). Every stand was located on post-agricultural land characterized by sandy, acidic or slightly acidic soils, with no calcium carbonates and low soil organic matter content in upper soil horizons (rusty soil—Arenosol). The distance between stands was at least 50 m. Finally, eight circular study plots (0.02 ha) were established in total. The study site characteristics were done in summer 2021 to note all plant species growing on each site. On each study plot, we measured: (1) the total number of trees (N); (2) the height of the trees (m); (3) the dimension at breast height—DBH (cm). Moreover, all vascular plants were recorded and the cover of each species in each layer was estimated using the seven-level Braun-Blanquet abundance scale (Table 4 in Appendix 1).

Soil analyses

The soil environment was characterized by the description of soil pit (at least to a depth of 1 m) located in the middle of the chosen stands. Subsequently, we described the reference soil groups based on the IUSS WRB (2015) and took soil and litter (mineral and organic layer separately) samples (ca. 500 g in total) from every soil horizon for further laboratory studies (16 samples in total). Soil samples were collected to determine: (1) soil texture (Casagrande’s aerometric method modified by Prószyński); (2) pH of soil and litter—measured in distilled water (potentiometric method); (3) content of organic carbon (Corg%—Tiurin’s method); (4) soil organic matter (SOM%—loss on ignition method); (5) the total nitrogen content (N%—Kjeldahl’s method); (6) C to N ratio; (7) elements such as Mg, Na, Ca, P, K (%) as well as Fe, Cd, Pb, Mn, Zn, and Cu (mg/kg) using atomic absorption spectrometry analysis using the AAS Varian 55B spectrometer (Peña et al. 2016). Moreover, we collected samples of intact soil for analysis of bulk density (BD; g/cm^3)—core method, and actual soil moisture (SM; %)—gravimetric method (Lityński et al. 1976). The analyses were conducted in the laboratory at the Poznań University of Life Sciences (Table 5 in Appendix 2).

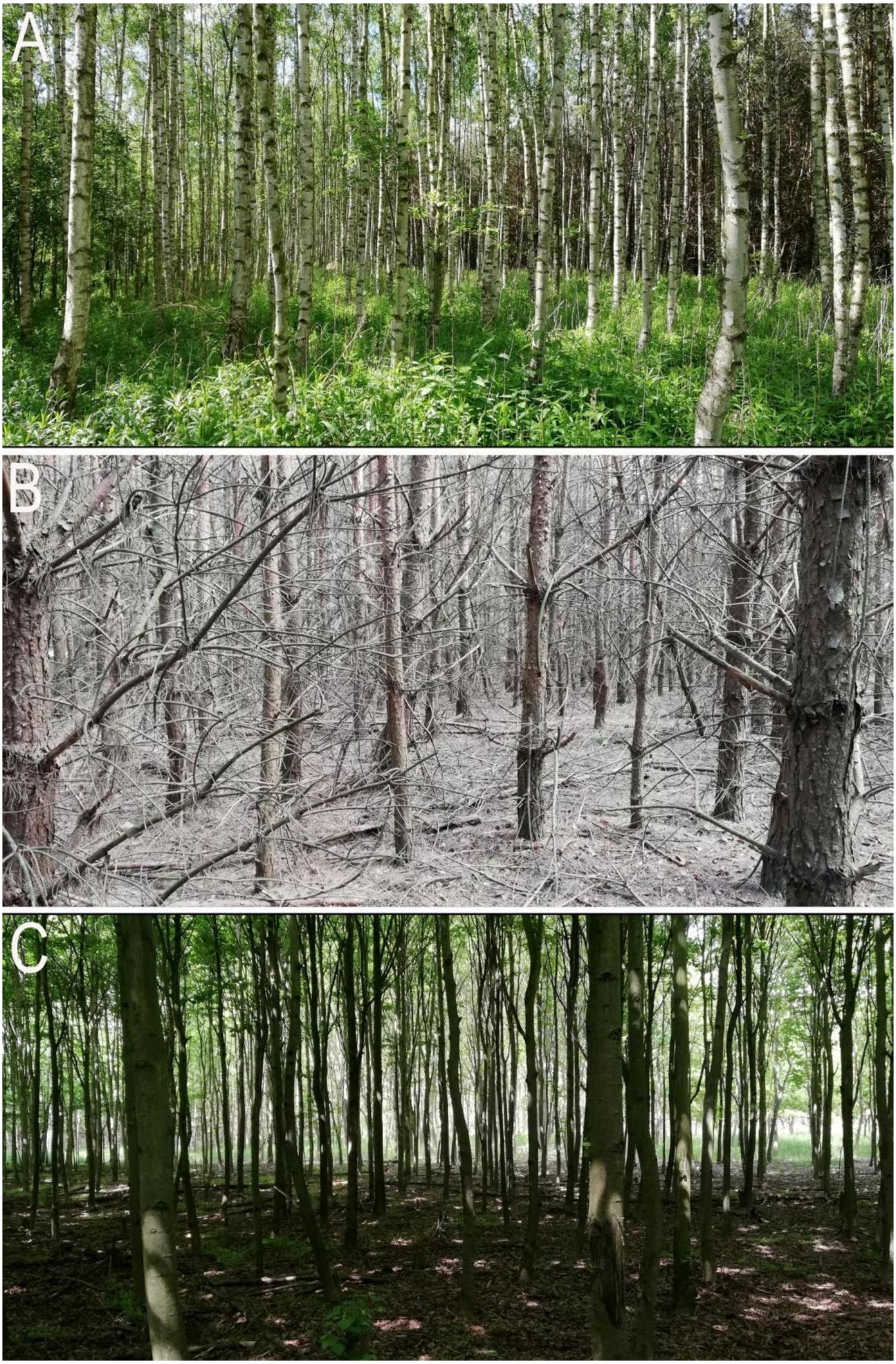

Fig. 1 Study sites on post-agricultural lands (July 2021) in the Opole Forest District: **A** *Betula pendula* stand, **B** *Pinus sylvestris* stand, **C** *Tilia cordata* stand

Mesostigmata mites investigation

Sampling was carried out four times: in July and October 2021 and in July and October 2022. Collecting of the soil samples (288 samples in total = eight plots × nine samples per plot × four samplings) was conducted on each study plot using metal soil corer (ø 5 cm) to the depth of 15 cm. In the laboratory, samples were placed on the Berlese-Tullgren apparatus, consisting of a funnel, a light bulb (40W), a strainer (mesh size 2 mm), and containers with 75% ethanol solution. Edaphon was extracted from the soil samples for at least seven days (until the collected samples were dry). Mesostigmatid mite individuals were selected from the alcohol solution under a stereomicroscope and placed in the Hoyer's medium on slides. The detailed diagnosis took place under a compound microscope Zeiss Axio Scope.A1. All individuals were classified into the appropriate instar, as well as species level or higher taxonomic unit using identification keys (Micherdziński 1969; Karg 1971, 1993; Gwiazdowicz 2007; Mašán & Halliday 2014).

Data analysis

Sampled material allowed to determine mite abundance (ind.), species richness and Shannon–Wiener diversity index ($H' = -\Sigma pi\ln(pi)$, where pi is the proportion of particular species in the mite community) for each of the plots. During analysis raw, data for abundance, species richness and diversity of mesostigmatid mite communities were presented as mean (± SE) values per sample within collection month and habitat type. In addition, for each species, indicators of dominance and constancy (the ratio of samples in which a given species occurs to all samples collected in a given variant) were determined for each habitat variant. Statistical analyses were done using R software (R version 4.1.2; R Core Team R: A Language and Environment for Statistical Computing; available online: https://www.r-project.org/). We used generalized linear models (GLM) assuming a Tweedie distribution for mesostigmatid abundance, species richness, and diversity calculated per sample and per plot. We applied predictors in models with low variance inflation factors (VIF < 5). Furthermore, we conducted Tukey post-hoc tests for each model to determine the differences in studied factors between month/habitat combinations. The statistical significance of variables used in GLM's was calculated using t-values. Results were treated as significant when $p < 0.05$. In order to describe the relationship between mesostigmatid mite assemblages and habitat characteristics, including soil properties, we conducted canonical correspondence analysis (CCA) implemented in the *vegan* package in R. The variables included in the CCA final model were based on Akaike information criterion (AIC). Furthermore, environmental variables were selected on VIF < 2. To test the factor's significance, we conducted a permutational analysis of variance (PERMANOVA). We plotted a cumulative species number using the vegan::specaccum() function (Oksanen et al. 2018). Furthermore, we used the bipartite package to reveal the relationship between mesostigmatid mite taxa and habitats (Dormann et al. 2008). In the conducted bipartite interaction network we assumed habitats as lower-level and mite taxa as higher-level groups. The taxa level response to specific habitat was described by specialisation index d′, derived from the Kulback-Leibler distance, expressing whether a given taxon is a non-specialist or a perfect specialist (range from 0 to 1). Additionally, d′ index describes how strongly the taxa differ from a random sampling of available interacting partners (Dormann 2011).

Results

Overall results

In total, 399 individuals (266 females, 50 males and 83 juveniles) were classified as 38 taxa (33 species, five genera) (Table 1). The GLM models assuming Tweedie distribution revealed that collection month and Fe content in soil affected abundance, species richness and diversity. Moreover, mesostigmatid mite abundance was influenced by litter N content (Table 2). The canonical correspondence analysis (CCA) revealed significant differences in mite taxa distribution. Axis 1 and axis 2 explained 26.1% and 25.0% of variance in community composition, respectively (Fig. 2). Axis 1 reflects collection time, while Axis 2 reflects the tree species studied. The analysis of variance conducted for the model showed that collection month ($p = 0.002$), year ($p = 0.002$), soil Mn content ($p = 0.001$), soil Na content ($p = 0.028$) and litter thickness ($p = 0.036$) significantly influenced the mite communities structure (Table 3). Species of the genus *Paragamasus* were influenced by soil Mn content and litter thickness. In contrast, species belonging to the genus *Veigaia* were affected by soil Na content and were also the least sensitive to soil Mn among all other genera.

Seasonal changes in mesostigmatid mite communities

The highest abundance calculated per sample was recorded in *P. sylvestris* stand in October 2022 (3.19 ± 0.62 ind.), while the lowest was recorded in *P. sylvestris* stand in July 2022 (0.37 ± 0.17). The highest abundance in July was reported in *T. cordata* stand in 2021 (1.59 ± 0.50 ind.) (Fig. 3A). The Tukey post-hoc tests revealed that mesostigmatid mite abundance was significantly lower in *P. sylvestris* stand in July (0.57 ± 0.17 ind.) than in *P. sylvestris* and *T. cordata* stands in October (2.17 ± 0.41 and 2.15 ± 0.34, respectively). Moreover, abundance in *P. sylvestris* stand in October was significantly higher than in *B. pendula* stand in July (0.78 ± 0.18 ind.).

The highest species richness per sample was recorded in *P. sylvestris* stand in October 2022 (1.85 ± 0.35 species) and the lowest in *P. sylvestris* stand in July 2022 (0.30 ± 0.12) (Fig. 2B). Species richness of mesostigmatid mite communities was significantly lower in *P. sylvestris* stand in July (0.52 ± 0.15 species) than in *P. sylvestris* and *T. cordata* stands in October (1.37 ± 0.25 and 1.37 ± 0.19, respectively) (Fig. 3B).

The highest mesostigmatid mite Shannon's diversity was found in *P. sylvestris* stand in October 2022 (0.52 ± 0.11), while the lowest was in *T. cordata* stand in July 2022 (0.05 ± 0.03). A significantly higher diversity was found in *P. sylvestris* stand in October (0.40 ± 0.07) compared to *P. sylvestris* and *B. pendula* stands in July (0.12 ± 0.05 and 0.14 ± 0.05, respectively) (Fig. 3C).

Mite communities structure

Most mite individuals belonged to the Parasitidae (111 ind.), Laelapidae (95) and Veigaiidae (70) families (Table 1). The most abundant species were *Hypoaspis* (*Gaeolaelaps*) *aculeifer* (21.6% of all recorded mites), *Veigaia nemorensis* (7.8%) and *Trachytes aegrota* (7.0%). Each of these species was most abundant in the *T. cordata* stand in October. Only two species occurred in each studied variant – *Veigaia nemorensis* and *Hypoaspis aculeifer*, while 15 mite species were unique for one variant (Fig. 4, Table 6 in Appendix 3). The cumulative species richness for *T. cordata* stand in October and July exceeded those for other examined month/habitat combinations (Fig. 5). The lowest juvenile abundance was recorded in *T. cordata* stand in July 2022 (0.07 ± 0.05 ind.; 2.4% of all juveniles). However,

Table 1 Species composition, dominance, and constancy of occurrence of individual mite species in each type of tree stand

No.	Mite taxa	*Betula pendula*			*Tilia cordata*			*Pinus sylvestris*		
		Individuals number	Dominance (%)	Constancy	Individuals number	Dominance (%)	Constancy	Individuals number	Dominance (%)	Constancy
1	*Alliphis halleri* (Canestrini & Canestrini, 1881)	0	0.00	0.00	1	0.58	0.01	0	0.00	0.00
2	*Amblyseius* spp.	1	1.27	0.01	5	2.91	0.05	0	0.00	0.00
3	*Antennoseius bacatus* Athias-Henriot, 1961	1	1.27	0.01	1	0.58	0.01	0	0.00	0.00
4	*Arctoseius venustulus* (Berlese, 1917)	1	1.27	0.01	1	0.58	0.01	0	0.00	0.00
5	*Asca aphidioides* (Linnaeus, 1758)	0	0.00	0.00	0	0.00	0.00	4	2.70	0.05
6	*Eugamasus cavernicola* (Trägårdh, 1912)	0	0.00	0.00	4	2.33	0.04	0	0.00	0.00
7	*Gamasellodes bicolor* (Berlese, 1918)	0	0.00	0.00	1	0.58	0.01	0	0.00	0.00
8	*Gamasellus montanus* (Willman, 1936)	1	1.27	0.01	1	0.58	0.01	0	0.00	0.00
9	*Hypoaspis* (*Gaeolaelaps*) *aculeifer* (Canestrini, 1883)	16	20.25	0.17	41	23.84	0.31	29	19.59	0.22
10	*Hypoaspis* spp.	2	2.53	0.01	5	2.91	0.02	0	0.00	0.00
11	*Hyposapis* (*Gaeolaelaps*) *praesternalis* (Willmann, 1949)	0	0.00	0.00	2	1.16	0.01	0	0.00	0.00
12	*Leptogamasus suecicus* (Trägårdh, 1936)	5	6.33	0.03	0	0.00	0.00	0	0.00	0.00
13	*Leptogamasus tectegynellus* (Athias Henriot, 1967)	0	0.00	0.00	2	1.16	0.01	0	0.00	0.00
14	*Macrocheles montanus* (Willmann, 1951)	4	5.06	0.04	8	4.65	0.06	0	0.00	0.00
15	*Macrocheles* spp.	2	2.53	0.01	0	0.00	0.00	0	0.00	0.00
16	*Olodiscus minima* (Kramer, 1882)	3	3.80	0.04	3	1.74	0.04	2	1.35	0.02
17	*Oodinychus ovalis* (C.L.Koch, 1839)	10	12.66	0.03	11	6.40	0.05	1	0.68	0.01
18	*Pachyseius humeralis* (Berlese, 1910)	0	0.00	0.00	1	0.58	0.01	0	0.00	0.00
19	*Paragamasus conus* (Karg 1971))	1	1.27	0.01	12	6.98	0.11	13	8.78	0.11

Table 1 (continued)

No.	Mite taxa	*Betula pendula*			*Tilia cordata*			*Pinus sylvestris*		
		Individuals number	Dominance (%)	Constancy	Individuals number	Dominance (%)	Constancy	Individuals number	Dominance (%)	Constancy
20	*Paragamasus jugincola* (Athias Henriot, 1967)	0	0.00	0.00	0	0.00	0.00	1	0.68	0.01
21	*Paragamasus runcatellus* (Berlese, 1903 sensu Karg 1971)	5	6.33	0.04	2	1.16	0.02	7	4.73	0.07
22	*Paragamasus* spp.	1	1.27	0.01	3	1.74	0.01	12	8.11	0.10
23	*Paragamasus vagabundus* (Karg, 1968)	2	2.53	0.03	1	0.58	0.01	19	12.84	0.11
24	*Pergamasus barbarus* (Berlese, 1904)	0	0.00	0.00	4	2.33	0.04	1	0.68	0.01
25	*Pergamasus crassipes* (Linnaeus, 1758)	0	0.00	0.00	1	0.58	0.01	1	0.68	0.01
26	*Pergamasus mediocris* Berlese, 1904	0	0.00	0.00	2	1.16	0.00	0	0.00	0.00
27	*Pergamasus septentrionalis* (Oudemans, 1902)	1	1.27	0.01	6	3.49	0.04	2	1.35	0.01
28	*Pergamasus* spp.	1	1.27	0.01	2	1.16	0.02	1	0.68	0.01
29	*Rhodacarus mandibularis* (Berlese, 1921)	0	0.00	0.00	0	0.00	0.00	1	0.68	0.01
30	*Trachytes aegrota* (C.L.Koch, 1841)	0	0.00	0.00	18	10.47	0.11	10	6.76	0.10
31	*Veigaia cerva* (Kramer, 1876)	0	0.00	0.00	0	0.00	0.00	1	0.68	0.01
32	*Veigaia decurtata* (Athias Henriot, 1961)	1	1.27	0.01	2	1.16	0.01	7	4.73	0.04
33	*Veigaia exigua* (Berlese, 1916)	11	13.92	0.07	5	2.91	0.05	10	6.76	0.09
34	*Veigaia nemorensis* (C.L.Koch, 1839)	9	11.39	0.08	18	10.47	0.19	4	2.70	0.05
35	*Veigaia planicola* (Berlese, 1892)	1	1.27	0.01	0	0.00	0.00	1	0.68	0.01
36	*Vulgarogamasus kraepelini* (Berlese, 1904)	0	0.00	0.00	1	0.58	0.01	0	0.00	0.00
37	*Zercon peltatus* (C.L.Koch, 1836)	0	0.00	0.00	8	4.65	0.06	18	12.16	0.16
38	*Zercon hungaricus* (Sellnick, 1958)	0	0.00	0.00	0	0.00	0.00	2	1.35	0.01
39	*Zercon triangularis* (C.L.Koch, 1836)	0	0.00	0.00	0	0.00	0.00	1	0.68	0.01

Table 2 Generalized linear models assuming a Tweedie distribution explaining mite abundance, species richness, and Shannon's diversity

Abundance					Species richness				Diversity			
Term	Estimate	SE	t value	Pr(>|t|)	Estimate	SE	t value	Pr(>|t|)	Estimate	SE	t value	Pr(>|t|)
(Intercept)	24.8773	11.9204	2.087	**0.049**	24.4813	9.8568	2.484	**0.021**	27.1233	12.6038	2.152	**0.043**
tree_PS	−0.9236	1.1251	−0.821	0.421	−0.4704	0.9547	−0.493	0.627	−0.3591	1.2443	−0.289	0.776
tree_TC	−0.2537	0.5448	−0.466	0.646	−0.1508	0.4757	−0.317	0.754	−0.0808	0.6561	−0.123	0.903
coll_month	0.8957	0.2284	3.922	**< 0.001**	0.6762	0.1878	3.600	**0.002**	0.7645	0.2437	3.137	**0.005**
year_2022	0.0346	0.2145	0.161	0.874	−0.0606	0.1777	−0.341	0.736	−0.1496	0.2275	−0.658	0.518
som	−0.5677	0.4301	−1.320	0.201	−0.5964	0.3610	−1.652	0.113	−0.6977	0.4660	−1.497	0.149
fl_n	2.0189	1.2076	1.672	0.109	2.1843	1.0003	2.184	**0.040**	2.6937	1.2910	2.086	**0.049**
ph_litter	−0.7052	0.9492	−0.743	0.465	−0.4079	0.7937	−0.514	0.613	−0.5508	1.0080	−0.546	0.590
fl_ca	−2.7421	2.8281	−0.970	0.343	−3.5976	2.4797	−1.451	0.161	−4.3148	3.4930	−1.235	0.230
soil_fe	−0.0665	0.0319	−2.087	**0.049**	−0.0714	0.0259	−2.752	**0.012**	−0.0829	0.0324	−2.556	**0.018**

Analysis of Deviance (Type III tests)

Term	LR Chisq	Df	Pr(> Chisq)	LR Chisq	Df	Pr(> Chisq)	LR Chisq	Df	Pr(> Chisq)
tree	0.7028	2	0.704	0.2566	2	0.880	0.0855	2	0.958
coll_month	16.1624	1	**< 0.001**	13.7086	1	**< 0.001**	10.5735	1	**0.001**
year	0.0258	1	0.872	0.1165	1	0.733	0.4336	1	0.510
som	1.7972	1	0.180	2.8857	1	0.089	2.3942	1	0.122
fl_n	2.8380	1	0.092	4.9247	1	**0.027**	4.5450	1	**0.033**
ph_litter	0.5553	1	0.456	0.2657	1	0.606	0.3021	1	0.583
fl_ca	0.9459	1	0.331	2.1511	1	0.143	1.5817	1	0.209
soil_fe	4.3780	1	**0.036**	7.7242	1	**0.006**	6.8199	1	**0.009**

SE—standard error, *tree_PS*—*Pinus sylvestris*, *tree_TC*—*Tilia cordata*, *coll_month*—collection month, *year*—year of sampling, *som*—soil organic matter, *fl_n*—litter N content, *ph_litter*—litter pH, *fl_ca*—litter Ca content, *soil_fe*—soil Fe content

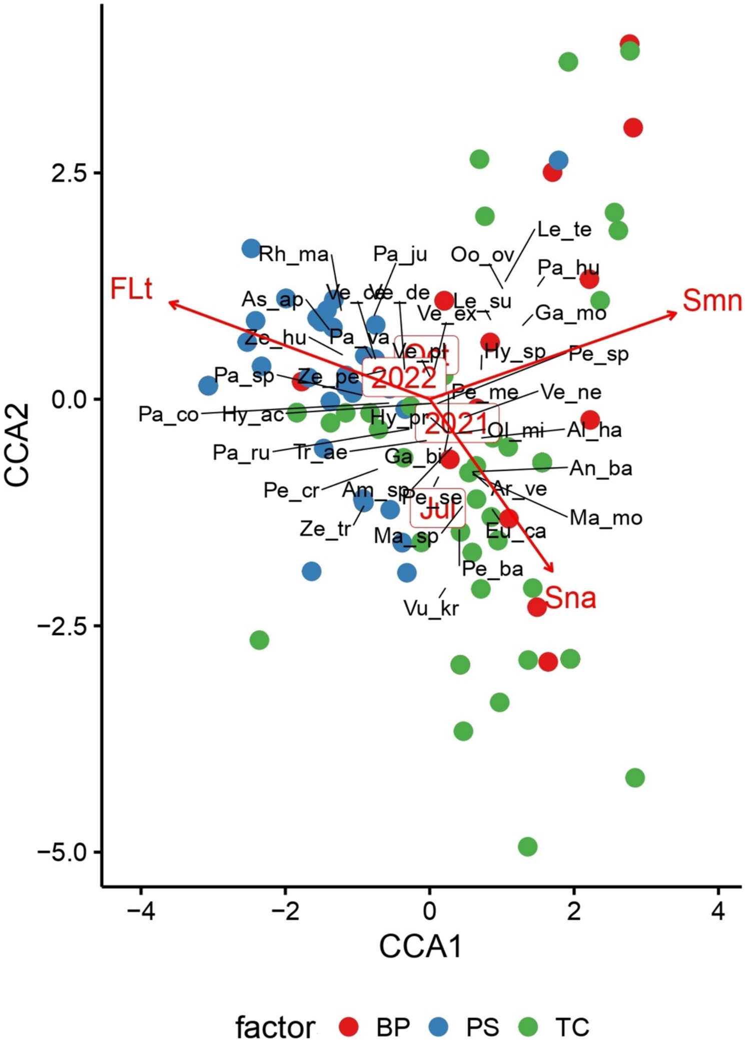

Fig. 2 Canonical correspondence analysis (CCA) for Mesostigmata communities across four sampling periods (July, October; 2020, 2021) in pure stands on post-agricultural lands (Opole Forest District). Mite taxa labelled with the first two letters of the genus name and the first two letters of the species name for each mite taxon (for abbreviations of mite taxa see Table 6 in Appendix 3). *BP*—*B. pendula*, *PS*—*P. sylvestris*, *TC*—*T. cordata*, *Jul*—July, *Oct*—October, *FLt*—forest litter thickness, *Sna*—soil Na content, Smn—soil Mn content

the number of juveniles was not statistically different among studied habitats and collection months (Fig. 3C). Interestingly, most females (2.19 ± 0.49 ind.; 22.2% of all females) were reported in *P. sylvestris* stand in October 2022, while the lowest female abundance was found in *P. sylvestris* stand in July of the same year (0.15 ± 0.09) (Fig. 6A). Males were the most numerous in the *T. cordata* stand in October 2022 (0.52 ± 0.20 ind.; 28.0% of all males). Moreover, no males were recorded in July 2022 in *T. cordata* and *B. pendula* stand (Fig. 4B). Furthermore, the most juveniles were found in *P. sylvestris* (0.56 ± 0.19 ind.;

Table 3 The influence of environmental variables on Mesostigmata communities (PERMANOVA)

Term	Df	ChiSquare	F	Pr(> F)
soil_mn	1	0.2707	1.9727	**0.001**
coll_month	1	0.2490	1.8147	**0.002**
year	1	0.2306	1.6803	**0.002**
fl_thickness	1	0.1991	1.4506	**0.036**
soil_na	1	0.2066	1.5054	**0.028**
Residual	125	17.1526		
Model	5	1.1559	1.6847	**0.001**
Residual	125	17.1526		

soil_mn soil Mn content, *coll_month* collection month, *year* year of collection, *fl_thickness* forest litter thickness, *soil_na* soil Na content

18.1% of all juveniles) and *T. cordata* stand (0.56 ± 0.15; 18.1%) in October 2022, as well as in *B. pendula* stand in October 2021 (0.56 ± 0.30; 12.1%) (Fig. 6C).

The largest number of *H. aculeifer* females was found in samples taken in October from the *P. sylvestris* and *T. cordata* stands (in both cases there were 22 individuals from two years, which accounted for 81.48% of all individuals of this species in the variant). In contrast, the largest number of *H. aculeifer* juveniles was found in samples taken in July from the *T. cordata* stand (6 ind.; 42.86%). Similarly, in the case of *V.nemoresnis*, the most females were found in samples collected in October from the *T.cordata* stand (10 ind.; 83.33%), while the most juvenile stages were reported in July in the *T. cordata* stand (4 ind.; 66,67%). No *T. aegrota* individuals were found in *B. pendula* stands, while the highest number of individuals of this species was reported in the *T. cordata* stands in October (35.71% of all *T. aegrota* individuals in total).

Discussion

Seasonal changes in mite communities

Generally, we found a significantly higher abundance of Mesostigmata mites in October than in July, as we expected from the results of other studies (Fujii and Takeda 2017). It alludes to the study by Kaczmarek et al. (2011), highlighting that soil moisture is the main factor that allows soil mite assemblage to develop. Indeed, in the climatic conditions of Poland, lower abundance in July may be explained by higher temperature and rapidly decreasing soil moisture in summer, which causes a decrease in mite density. With the end of summer, the temperature remains high, but soil moisture increases. Consequently, this causes an increase in soil mite density (Salmane 2000). The same relationship also applied to species richness and diversity of soil acarofauna. Similar importance of precipitation and temperature for the soil mite community structure was also revealed by Kamczyc et al. (2022), who reported that the abundance of mesostigmatid mites in decomposing litter of broadleaved and coniferous temperate tree species was positively correlated with the temperature of the sampling month and negatively correlated with the temperature of the month before sampling. The difference with our study was that the abundance shown in summer (July) was higher than in autumn (October). Species richness and diversity showed only slight changes between consecutive months of the growing season (April–October).

An interesting result of our study is the increase in the proportion of juvenile instars in summer. They are considered to be more sensitive than adult mite instars to temperature increases and humidity decreases, which is associated *inter alia* with a lower degree

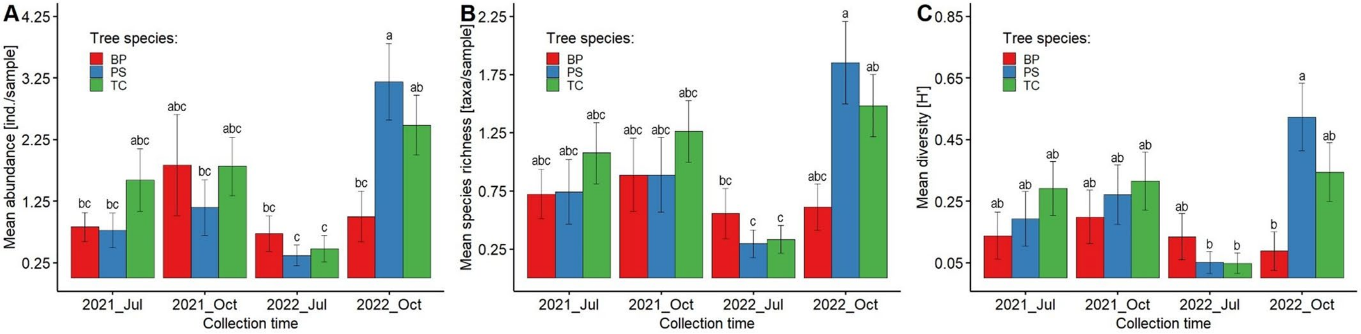

Fig. 3 Mean abundance (**A**), species richness (**B**) and Shannon's diversity (**C**) of mesostigmatid mites in the total communities across four sampling periods (July, October; 2020, 2021) in pure stands on post-agricultural lands (Opole Forest District). Abbreviations of variants: *Oct*—October, *Jul*—July, *BP*—*B. pendula*, *PS*—*P. sylvestris*, *TC*—*T. cordata*, *Oct_PS*—October/*P. sylvestris*, *Jul_PS*—July/*P. sylvestris*, *Oct_TC*—October/*T. cordata*, *Jul_BP*—July/*B. pendula*, *Jul_TC*—July/*T. cordata*, *Oct_BP*—October/*B. pendula*

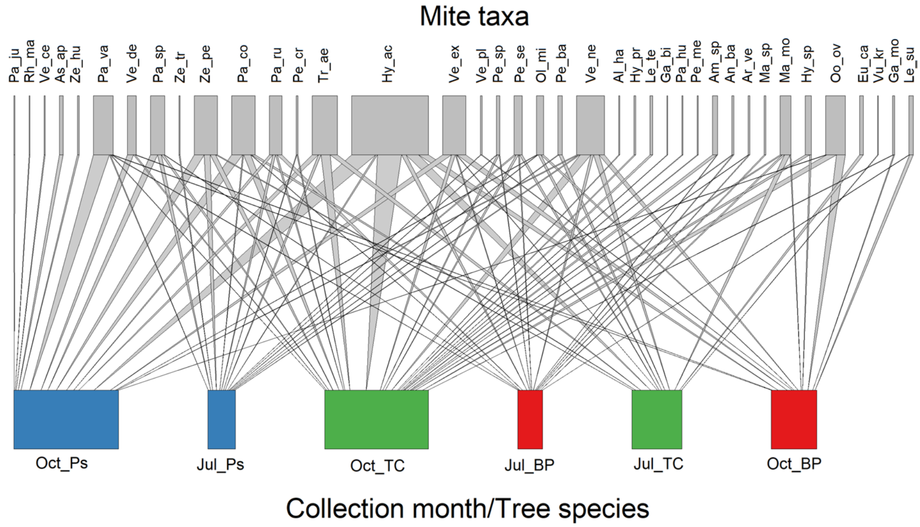

Fig. 4 Co-occurrence network for bipartite relationships between mesostigmatid mite taxa (upper boxes) and collection Month/Habitat (lower boxes). Boxes are proportional to total mite abundance, whereas ribbon width is proportional to the co-occurrence. *Oct_PS*—October/*P. sylvestris*, *Jul_PS*—July/*P. sylvestris, Oct_TC*—October/*T. cordata*, *Jul_BP*—July/*B. pendula*, *Jul_TC*—July/*T. cordata*, *Oct_BP*—October/*B. pendula*. For abbreviations of mite taxa see Table 6 in Appendix 3

of body sclerotization (Huhta and Hänninen 2001). Adult mites should be more resistant than juveniles to water loss and less susceptible to changes in temperature and humidity (Urbanowski et al. 2021). An explanation for our result may be the overlap of the period of high mortality with the hatching of mesostigmatid juveniles. As demonstrated by Kaczmarek et al. (2011), under similar climatic conditions, there are two density peaks for mesostigmatid mites—in January and at the turn of spring and summer.

Most identified individuals belonged to the Parasitidae, Laelapidae and Veigaiidae families. Mites of the Parasitidae family are found in all types of forests, meadows, bogs, and farmland. They mainly inhabit the litter but also the humus layer. Their main prey are springtails and other mites, such as Oribatida and Astigmata (Błoszyk 2008). The Laelapidae family includes, among others, large predatory species of the *Hypoaspis* genus. *Hypoaspis* (*Geolaelaps*) *aculeifer* is a common pioneer species (Wissuwa et al. 2012), also found in large numbers on former farmland. *Hypoaspis aculeifer* is a species that *inter alia* preys on springtails (Cortet et al. 2003). Veigaiidae family contains species specialised in feeding on springtails, but may also feed on other soil fauna (Koehler 1999). They primarily inhabit forest litter in the Palearctic but are also found in meadows and agricultural land (Błoszyk 2008). Together with the mites of the Parasitidae family, they form the dominant group of predators in the Mesostigmata order (Koehler 1997; Błoszyk 2008; Skorupski 2008; Kazemi et al. 2013). *Veigaia nemorensis* is a common species in the litter and upper soil layers on former farmland and even on degraded or post-industrial sites (Skorupski et al. 2013; Manu et al. 2017). *Veigaia nemorensis*, in contrast to the general characteristics of the Veiigaidae family, mainly preys on bacterial and root-feeding nematode species (Manu et al. 2017).

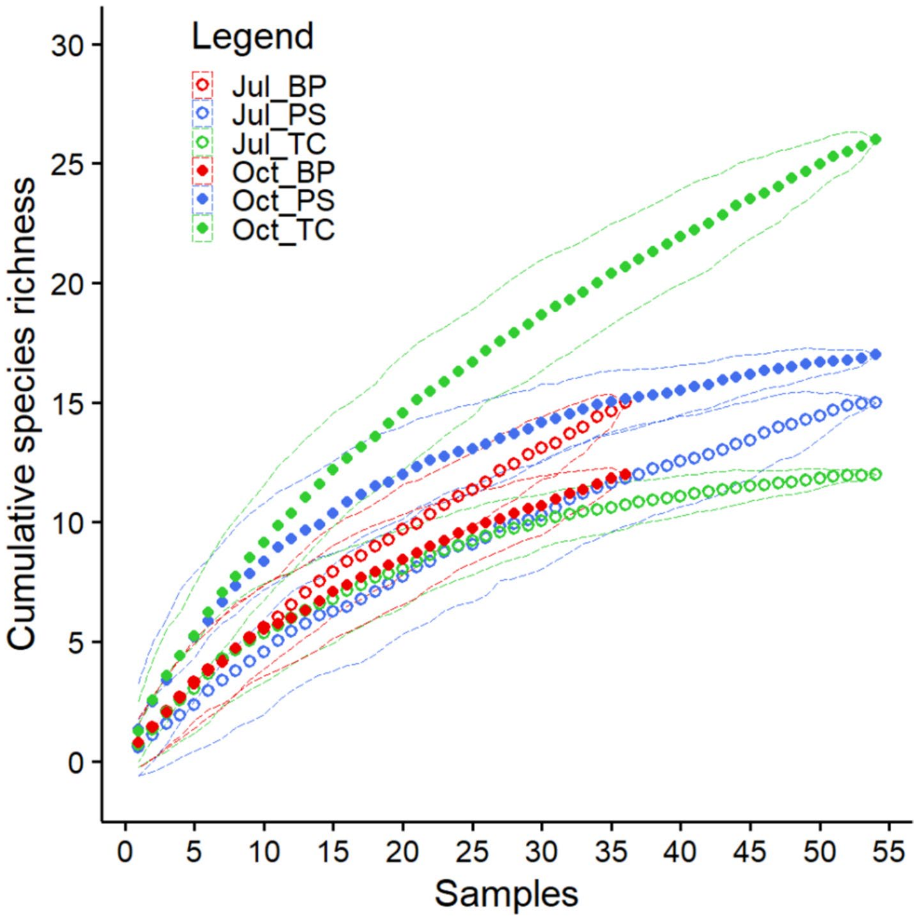

Fig. 5 Cumulative species richness (data presented as mean values) for each month/habitat examined. *Oct_PS*—October/*P. sylvestris*, *Jul_PS*—July/*P. sylvestris*, *Oct_TC*—October/*T. cordata*, *Jul_BP*—July/*B. pendula*, *Jul_TC*—July/*T. cordata*, *Oct_BP*—October/*B. pendula*

Tree species impact

The differences in litter impact of tree species such as *P. sylvestris*, *B. pendula and T. cordata* on mesostigmatid mite assemblages were compared by Kamczyc et al. (2019) and Urbanowski et al. (2021). Kamczyc et al. (2019) showed that tree litter only affected abundance, while there was no influence on species richness and diversity of mesostigmatid mite assemblages. In addition, they indicated a positive effect of *P. sylvestris* litter comparing to *T. cordata* litter on soil mite density. In contrast, Urbanowski et al. (2021) showed no significant differences in the effect of *P. sylvestris* and *B. pendula* litter on the abundance, species richness and diversity of mesostigmatid mite communities. Our study did not show differences in the influence of individual tree species on the soil Mesostigmata. However, when comparing mite assemblages in summer and autumn, we observed high differences in mite abundance, species richness and diversity between the studied stands. Our results indicate that the most extreme abundance values were found in *P. sylvestris* stand, which provided the most favourable conditions for the soil fauna in autumn and the least favourable in summer. This effect may be explained by the highest water absorption

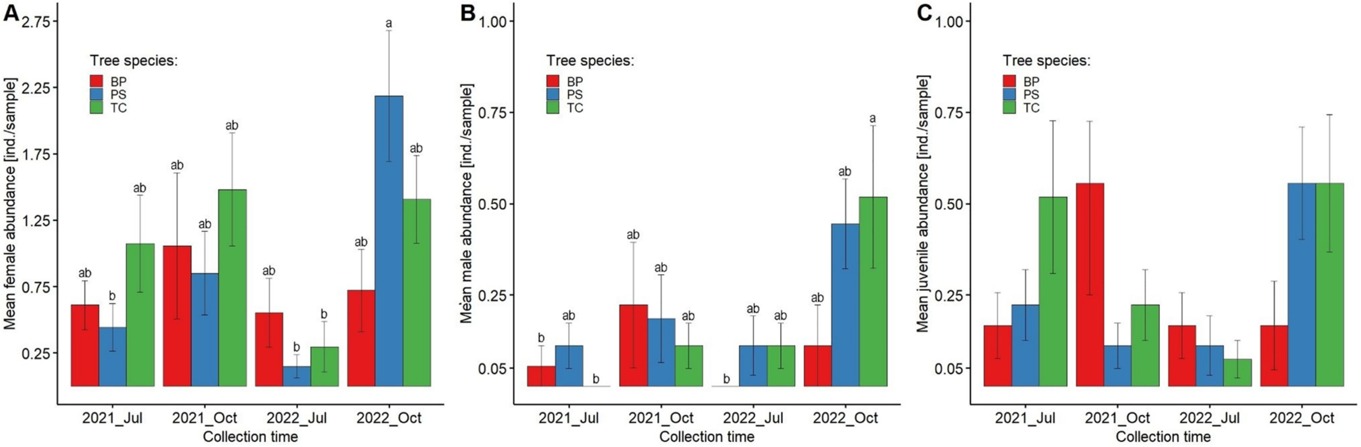

Fig. 6 Mean female (**A**), male (**B**) and juvenile (**C**) abundance of mesostigmatid mite communities across four sampling periods (July, October; 2020, 2021) in pure stands on post-agricultural lands (Opole Forest District).. *Oct*—October, *Jul*—July, *BP*—*B. pendula*, *PS*—*P. sylvestris*, *TC*—*T. cordata*

capacity of *P. sylvestris* litter, a coniferous species, with the greatest decreases in moisture during dry months (Zhou et al. 2018). Interestingly, Ilek et al. (2024) revealed that forest litter with a low C:N ratio and a predominant share of oak leaves achieved the greatest water storage capacity, while litter with a high C:N ratio and a predominant share of *P. sylvestris* needles had the lowest water storage capacity. This is consistent with our results because the C:N ratio was the lowest in the *P. sylvestris* stand and the highest in the *T. cordata* stand. Also in the *B. pendula* stand, mite abundance and diversity were significantly lower in summer than in *P. sylvestris* stand in autumn. We assume that this results from the fact that *B. pendula* stands are less able to protect the soil in summer from heating and drying out (Jonczak et al. 2020).

Interaction between soil parameters and mite communities

Our study revealed that Fe content in soil affected abundance, species richness and diversity of mite communities—the biodiversity decreased as soil Fe concentration increased. The negative effects of this nutrient on soil fauna were also noted by Huot et al. (2018) and Rusek and Marshall (2000). An increase in soil Fe concentration may limit the development of springtails, reduce manganese uptake, and stress soil organisms through the energy-demanding detoxification process (Rusek and Marshall 2000). Christophe et al. (2014) proved that the concentration of elements such as Fe in the rhizosphere solution and the soil environment changes with the seasons and is highest in autumn. Widowati and Sukristyonubowo (2019) showed that Fe becomes less toxic to plants when the soil pH is lower. In turn, Thoms and Gleixner (2013) observed that soil pH is lower in autumn than in summer.

Also, the collection month significantly affected the abundance, species richness and diversity of mesostigmatid mite communities. Changes in weather conditions with the ongoing seasons appear to be crucial to the density and diversity of soil fauna communities. This is not surprising because mites are ectothermic organisms, depending on climatic conditions such as temperature and precipitation (Thakur et al. 2018). This result was also confirmed by other studies conducted in central Europe (Urbanowski et al. 2021; Kamczyc et al. 2022). Additionally, species richness and diversity of mesostigmatid mites increased with litter nitrogen content, which may be associated with a higher biomass and species richness of microorganisms and nematodes (Kaneko and Salamanca 1999; Sánchez-Moreno et al. 2009; Renčo et al. 2020). Interestingly, in our study, the abundance of mites was not influenced by litter nitrogen content, which is correlated with the type of litter (Cornwell et al. 2008; Horodecki and Jagodziński 2019). It corresponds to the conclusions of studies conducted by Seniczak et al. (2018) on moss mite (Oribatida) and mesostigmatid mite communities. They reported that nutrient-rich habitats generate high species diversity but low densities of soil mites. This may mean that poorly fertile habitats have the opposite trend in mite community structure.

Conclusions

In conclusion, we revealed that different tree species growing on post-agricultural lands shape various soil conditions, which change between the summer and autumn seasons. Large fluctuations in soil mite abundance, species richness and diversity between *P. sylvestris* and *B. pendula* stands in summer and autumn may depend on tree species and season, which may constitute proof for using mixed stands during afforestation of post-agricultural lands. Seasonal change in the proportion between instars was unclear, but contrary to expected results, the proportion of young individuals increased in summer.

Appendix 1

See Table 4.

Table 4 Stand characteristic for each study plot

Study plot	Forest stand	Age of forest stand [Years]	Number of trees [N/ha]	Avg. DBH [mm]	SD Dbh [mm]	Avg. height [m]	SD height [m]	Basal area [m^2/ha]	Volume of gross timber [m^3/ha]	Coverage and species of tree layer [%]	Coverage and species of shrub layer [%]	Coverage and species of vascular ground layer [%]	Coverage and species of bryophytes ground layer [%]
1	*T. cordata*	22	3500	**96**	28	**10.0**	1.0	**27.5**	**95**	100 T. *cordata*	10 T. *cordata*	30 V. *hederifolia*	–
2	*T. cordata*		2900	**104**	29	**11.1**	1.1	**26.4**	**115**	100 T. *cordata*	10 T. *cordata*	50 V. *hederifolia*	–
3	*T. cordata*		3950	**80**	23	**8.3**	1.5	**21.6**	**52**	100 T. *cordata*	20 T. *cordata*	40 V. *hederifolia*	–
4	*B. pendula*		2350	**121**	29	**16.5**	2.0	**28.5**	**224**	80 *B. pendula*	–	40 *S.canadensis*, 20 *G. aparine*, 10 *U. dioica*, 10 *C. arundinacea*, 10 V. *hederifolia*	30 *P. schreberi*
5	*B. pendula*		1700	**123**	32	**15.1**	2.0	**21.4**	**159**	70 *B. pendula*	10 *C. monogyna*	40 *S. canadensis*, 20 V. *hederifolia*, 10 *C. arundinacea*, 10 *U. dioica*, 10 *G. aparine*	10 *P. schreberi*
6	*P. sylvestris*		2500	**144**	38	**14.7**	0.6	**43.5**	**307**	90 *P. sylvestris*	–	–	50 *P. schreberi*
7	*P. sylvestris*		2850	**124**	38	**13.7**	1.0	**37.7**	**253**	90 *P. sylvestris*	–	–	40 *P. schreberi*
8	*P. sylvestris*		2800	**127**	37	**13.8**	1.2	**38.2**	**260**	100 *P. sylvestris*	–	–	10 *P. schreberi*

SD—standard deviation, *T. cordata—Tilia cordata, B. pendula—Betula pendula, P. sylvestris—Pinus sylvestris, C. monogyna—Crataegus monogyna, V. hederifolia—Veronica hederifolia, S. canadensis—Solidago canadensis, G. aparine—Galium aparine, U. dioica—Urtica dioica, C. arundinacea—Calamagrostis arundinacea, P. schreberi—Pleurozium schreberi*

Appendix 2

See Table 5.

Table 5 Soil properties for each study plot

Plot	Tree species	Soil texture	Litter pH	Litter thickness (cm)	Soil pH	$CaCO_3$ (%)	SOM (%)	Corg (%)	Bulk density (g/cm^3)	Soil moisture (%)	Soil N (%)	Litter N (%)	Soil Mg (%)	Litter Mg (%)	Soil Ca (%)	Litter Ca (%)
1	TC	S	5.36	1.5	5.03	0	3.41	1.98	1.631	8.0	0.190	1.819	0.1919	0.2075	0.0220	0.1874
2	TC	S	5.68	1.5	4.66	0	2.43	1.41	1.308	7.1	0.238	1.907	0.1930	0.2095	0.0029	0.1952
3	TC	S	5.47	1.4	4.72	0	2.09	1.21	1.436	8.1	0.221	1.503	0.1883	0.2104	0.0100	0.1936
4	BP	S	5.68	1.7	4.11	0	1.89	1.10	1.404	4.6	0.170	1.486	0.1824	0.2078	0.0011	0.1812
5	BP	S	5.63	1.6	4.24	0	2.03	1.18	1.411	4.5	0.150	1.605	0.1858	0.0000	0.0003	0.0000
6	PS	S	4.63	2.9	3.51	0	1.79	1.04	1.498	1.9	0.143	1.513	0.1841	0.2021	0.0014	0.1787
7	PS	S	4.51	3.3	3.52	0	1.14	0.66	1.436	1.3	0.129	1.601	0.1890	0.2020	0.0036	0.1826
8	PS	S	4.9	2.9	4.02	0	1.39	0.81	1.547	3.8	0.146	1.411	0.1833	0.2025	0.0031	0.1669
Plot	Soil Na (%)	Litter Na (%)	Soil K (%)	Litter K (%)	Soil Fe (mg/kg)	Litter Fe (mg/kg)	Soil Cd (mg/kg)	Litter Cd (mg/kg)	Soil Pb (mg/kg)	Litter Pb (mg/kg)	Soil Mn (mg/kg)	Litter Mn (mg/kg)	Soil Zn (mg/kg)	Litter Zn (mg/kg)	Soil Cu (mg/kg)	Litter Cu (mg/kg)
1	0.0024	0.0042	0.0137	0.0792	333.05	141.36	0.25	0.15	12,41	5.79	276.03	404.37	13.59	32.66	13.59	32.66
2	0.0027	0.0045	0.0068	0.0660	339.56	237.62	0.22	0.54	15,62	7.57	149.23	406.31	14.38	66.82	14.38	66.82
3	0.0029	0.0089	0.0146	0.0740	334.26	237.96	0.16	0.42	11,91	2.29	200.75	415.81	10.23	46.08	10.23	46.08
4	0.0023	0.0040	0.0060	0.0470	344.38	252.53	0.09	0.68	13,09	9.11	269.04	434.02	4.79	78.26	4.79	78.26
5	0.0029	0.0000	0.0067	0.0000	350.59	0.00	0.12	0.00	14,29	0.00	273.45	0.00	4.21	0,00	4.21	0.00
6	0.0025	0.0034	0.0044	0.0603	331.93	163,26	0.12	0.60	10,15	5.48	155.42	427.06	5.74	40.01	5.74	40.01
7	0.0023	0.0036	0.0148	0.0501	348.07	181.90	0.12	0.53	8,82	5.09	144.00	424.27	6.83	31.61	6.83	31.61
8	0.0019	0.0040	0.0049	0.0601	346.33	179.07	0.12	0.39	8,24	3.33	106.77	395.76	5.93	22.00	5.93	22.00

TC—Tilia cordata, *BP—Betula pendula*, *PS—Pinus sylvestris, S—Sand, SOM*—soil organic matter, *Corg*—organic carbon

Appendix 3

See Table 6.

Table 6 Network statistics for mesostigmatid mite taxa, describing their affiliation to habitats and specialisation

No	Mite taxa	Abbreviation	Number of habitats	Proportion of habitats	Species specificity index d′
1	*Alliphis halleri* (Canestrini & Canestrini, 1881)	Al_ha	1	0.17	1.000
2	*Amblyseius* spp.	Am_sp	2	0.33	0.817
3	*Antennoseius bacatus* Athias-Henriot, 1961	An_ba	2	0.33	0.633
4	*Arctoseius venustulus* (Berlese, 1917)	Ar_ve	2	0.33	0.633
5	*Asca aphidioides* (Linnaeus, 1758)	As_ap	1	0.17	1.000
6	*Eugamasus cavernicolus* Trägårdh, 1912	Eu_ca	1	0.17	1.000
7	*Gamasellodes bicolor* (Berlese, 1918)	Ga_bi	1	0.17	1.000
8	*Gamasellus montanus* (Willmann, 1936)	Ga_mo	2	0.33	0.633
9	*Hypoaspis* (*Geolaelaps*) *aculeifer* (Canestrini, 1883)	Hy_ac	6	1.00	0.305
10	*Hypoaspis* spp.	Hy_sp	2	0.33	0.714
11	*Hypoaspis* (*Geolaelaps*) *praesternalis* (Willmann, 1949)	Hy_pr	1	0.17	1.000
12	*Leptogamasus succineus* Witaliński, 1973	Le_su	2	0.33	0.785
13	*Leptogamasus tectegynellus* (Athias Henriot, 1967)	Le_te	1	0.17	1.000
14	*Macrocheles montanus* (Willmann, 1951)	Ma_mo	4	0.67	0.466
15	*Macrocheles* spp.	Ma_sp	1	0.17	1.000
16	*Olodiscus minima* (Kramer, 1882)	Ol_mi	4	0.67	0.418
17	*Oodinychus ovalis* (C.L.Koch, 1839)	Oo_ov	3	0.50	0.592
18	*Pachyseius humeralis* (Berlese, 1910)	Pa_hu	1	0.17	1.000
19	*Paragamasus conus* (Karg 1971)	Pa_co	5	0.83	0.449
20	*Paragamasus jugincola* (Athias Henriot, 1967)	Pa_ju	1	0.17	1.000
21	*Paragamasus runcatellus* (Berlese, 1903 sensu Karg 1971)	Pa_ru	4	0.67	0.361
22	*Paragamasus* spp.	Pa_sp	4	0.67	0.471
23	*Paragamasus vagabundus* (Karg, 1968)	Pa_va	5	0.83	0.783
24	*Pergamasus barbarus* (Berlese, 1904)	Pe_ba	2	0.33	0.785
25	*Pergamasus crassipes* (Linnaeus, 1758)	Pe_cr	2	0.33	0.633
26	*Pergamasus mediocris* Berlese, 1904	Pe_me	1	0.17	1.000
27	*Pergamasus septentrionalis* (Oudemans, 1902)	Pe_se	4	0.67	0.375
28	*Pergamasus* spp.	Pe_sp	3	0.50	0.500
29	*Rhodacarus mandibularis* (Berlese, 1921)	Rh_ma	1	0.17	1.000
30	*Trachytes aegrota* (C.L.Koch, 1841)	Tr_ae	4	0.67	0.374
31	*Veigaia cerva* (Kramer, 1876)	Ve_ce	1	0.17	1.000
32	*Veigaia decurtata* (Athias Henriot, 1961)	Ve_de	3	0.50	0.669
33	*Veigaia exigua* (Berlese, 1916)	Ve_ex	5	0.83	0.432
34	*Veigaia nemorensis* (C.L.Koch, 1839)	Ve_ne	6	1.00	0.302

Table 6 (continued)

No	Mite taxa	Abbreviation	Number of habitats	Proportion of habitats	Species specificity index d′
35	*Veigaia planicola* (Berlese, 1892)	Ve_pl	2	0.33	0.633
36	*Vulgarogamasus kraepelini* (Berlese, 1904)	Vu_kr	1	0.17	1.000
37	*Zercon peltatus peltatus* (C.L.Koch, 1836)	Ze_pe	4	0.67	0.416
38	*Zercon hungaricus* (Sellnick, 1958)	Ze_hu	1	0.17	1.000
39	*Zercon triangularis* (C.L.Koch, 1836)	Ze_tr	1	0.17	1.000

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Declarations

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