

## 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 error 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 stoichiometry, 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.isiwebknowledge.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 ( $\ln R$ ). 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 ( $X_t$  and  $X_c$ ), where  $X_t$  is the mean value of index (abundance, richness or Shannon diversity in our case) recorded from post-agricultural forest, and  $X_c$  is the mean value of the index on arable habitat.

$$\ln R = \ln \frac{X_t}{X_c} = \ln X_t - \ln X_c \quad (1)$$

The effect size of each data pair was obtained by meta-analysis, and the weighted mean effect size,  $\ln R_{++}$ , 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](http://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], heathlands [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]. Addition-

ally, mixed forests represent various plant communities, such as bog alder forest (*Ribes nigri-Alnetum*) and fresh coniferous forest (*Quercus 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 campestre-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 campestre-Quercetumpetraeae-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.

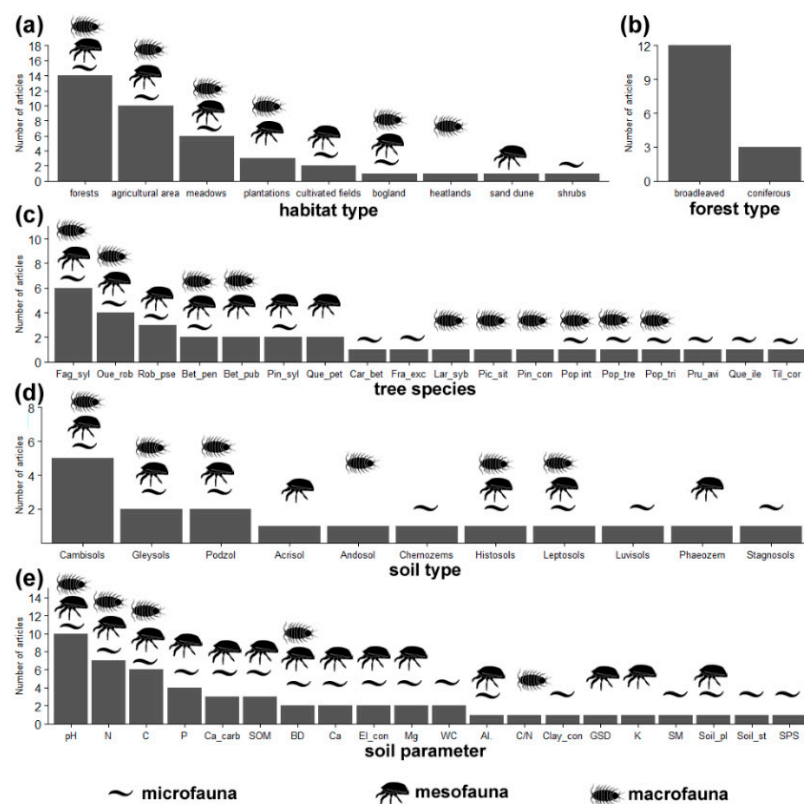
#### 4. Effect of Afforestation on Soil Chemistry

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).

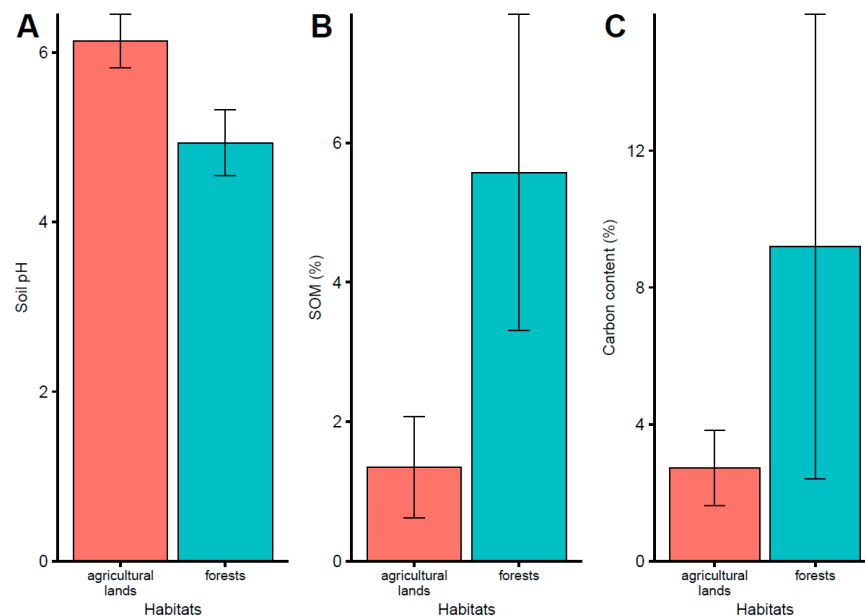


**Figure 1.** Habitat types (a), forest types (b), tree species (c), soil types (d) and soil parameters (e) reported from publications on post-agricultural sites. Tree species abbreviations are based on the first three letters of the genus and species name of the tree species. Soil parameter abbreviations 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 <sub>3</sub>	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 field, 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 <sub>3</sub>	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 ( $6.14 \pm 0.32$ ) than in forests ( $4.94 \pm 0.39$ ), and that the difference was significantly different ( $p < 0.01$ ). Additionally, soil organic matter was lower on agricultural lands ( $1.35 \pm 0.73$ ) than in forests ( $5.56 \pm 2.27$ ) but did not differ significantly ( $p > 0.05$ ). Further, our data analysis revealed that agricultural lands had lower carbon content ( $2.73 \pm 1.09$ ) than in forests ( $9.20 \pm 6.79$ ), 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 heathlands [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 and 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 ( $\text{NO}_3$ ) content in relict forests than in reforested sites or abandoned fields, compared to two-times-higher nitrogen ( $\text{NH}_4^+$ ) 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  $2\times$  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 heathlands, 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  $3.5\times$  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 stoichiometry 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

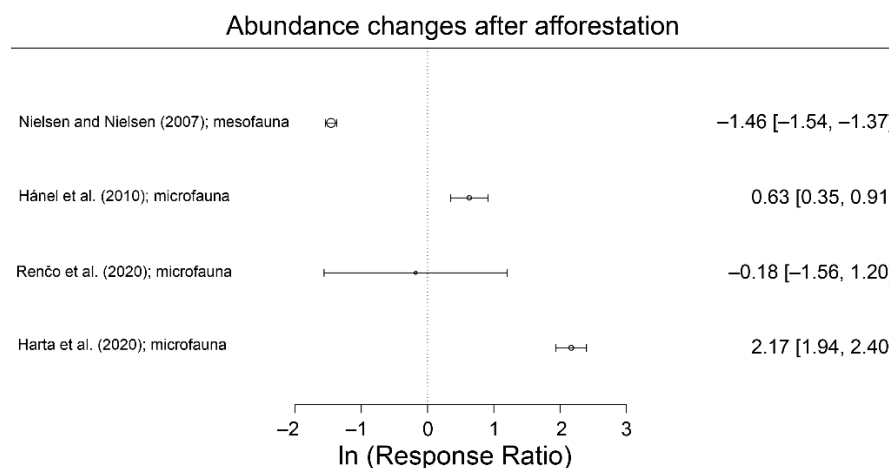
Soil biota plays an essential role in ecosystem functioning, especially in biogeochemical cycles with feedback on plant diversity, abundance, succession and productivity [44]. Soil fungi and bacteria break down organic matter using an arsenal of hydrolytic and lignolytic enzymes that provide available 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 et 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 et 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 et 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. Hanel [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  $1350 \times 10^3$  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 from 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 Lumbricidae 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<sub>3</sub> 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 field 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<sup>3</sup>). 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<sup>-1</sup>), 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 error 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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