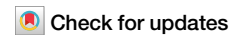


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Permaculture enhances carbon stocks, soil quality and biodiversity in Central Europe



Julius Reiff¹ , Hermann F. Jungkunst¹ , Ken M. Mauser¹, Sophie Kampel², Sophie Regending¹, Verena Rösch¹ , Johann G. Zaller² & Martin H. Entling¹

Permaculture is proposed as a tool to design and manage agroecological systems in response to the pressing environmental challenges of soil degradation, climate change and biodiversity loss. However, scientific evidence on the effects of permaculture is still scarce. In this comprehensive study on a wide range of soil and biodiversity indicators, we examined nine farms utilizing permaculture and paired control fields with locally predominant agriculture in Central Europe. We found 27% higher soil carbon stocks on permaculture sites than on control fields, while soil bulk density was 20% lower and earthworm abundance was 201% higher. Moreover, concentrations of various soil macro- and micronutrients were higher on permaculture sites indicating better conditions for crop production. Species richness of vascular plants, earthworms and birds was 457%, 77% and 197% higher on permaculture sites, respectively. Our results suggest permaculture as effective tool for the redesign of farming systems towards environmental sustainability.

Our world faces a series of urgent environmental challenges, such as soil degradation, biodiversity loss, and climate change. Agriculture is a major driver for transgressing planetary boundaries of biosphere integrity and biogeochemical flows, as well as for land-system change, freshwater use, and climate change being at high risk¹. On the other hand, agriculture is severely affected by these global change challenges^{2,3}. Hence, rapid and profound changes are required to maintain food security⁴ while mitigating climate change and restoring biodiversity on agricultural land⁵. A substantial contribution to climate change mitigation on agricultural land can be accomplished by increasing soil organic carbon by 4% or 0.6 t ha⁻¹ per year⁵. The process of transferring and storing CO₂ from the atmosphere into the soil as part of the soil organic matter, through plants or other organic solids, is called soil carbon sequestration⁶. It has substantial and technically feasible potential to stabilize the global climate system⁷. In addition, soils richer in carbon and, therefore, of higher quality can stabilize yields under variable climate⁸ and mitigate climate-driven declines in agricultural production⁸. Phosphorus is essential for crop production, while its rock resources are finite. Therefore improvements in phosphorus use efficiency are an immediate and urgent need⁹. A higher soil organic matter content improves the availability of phosphorus to crops¹⁰ and enables comparable yields with substantially lower soil phosphorus levels¹¹. In addition to nutritional

requirements, intact biodiversity is essential for agriculture and food production as greater agro-biodiversity can lead to higher resilience of yields to drought, disease outbreaks, or other stresses⁴. High and stable yields also reduce the need for land clearing and for the use of agrochemicals¹². Hence, the implementation of agroecological principles has been suggested as a viable way out of the negative feedback loops between agriculture and environmental change¹³. At the same time, agroecology is a methodical approach to meet the requirements of agricultural sustainability in terms of context-specificity, flexibility, and circular management¹⁴, with permaculture providing a framework for the design and management of agroecological systems^{15,16}.

Permaculture creates agriculturally productive ecosystems that mimic the diversity, stability, and resilience of natural ecosystems¹⁷. In this context, the term permaculture encompasses a set of agricultural practices, a design system to select, combine, and arrange those practices, and also the resulting agroecological farming system¹⁵. Permaculture systems are, therefore, highly individual and context-specific, which can be essential for a high degree of sustainability. As a result, it is not possible to establish fixed general guidelines as is the case for organic agriculture. Instead, both agroecology and permaculture are based on sets of principles or elements emphasizing a growing set of favorable agricultural practices¹⁶. There is a strong overlap in the principles

¹IES Landau, Institute for Environmental Science, RPTU Kaiserslautern-Landau, Fortstraße 7, 76829 Landau in der Pfalz, Germany. ²Institute of Zoology, Department of Integrative Biology and Biodiversity Research, University of Natural Resources and Life Sciences Vienna (BOKU), 1180 Vienna, Austria.

e-mail: julius.reiff@rptu.de

of these two approaches, which include the promotion of habitat, species, and genetic diversity, the cycling of biomass and nutrients, the build-up of storages of fertile soil and water, and the integration of different land use elements to create synergies¹⁶. Hereby, both permaculture and agroecology aim to establish regenerative agriculture in terms of environmental health^{18,19}. Furthermore, agroecology has an additional focus on social values, responsibility governance and solidarity economy, while permaculture shows a strong emphasis on the conscious design of such agroecosystems.

The United Nations Food and Agriculture Organization (FAO) proposes agroecology as a key approach to achieving the Sustainable Development Goals (SDG), especially to end hunger, achieve food security and improved nutrition, and promote sustainable agriculture (SDG No. 2)²⁰. However, permaculture has received little political or scientific attention while being spread around the world by practitioners and itinerant teachers^{15,21}. Permaculture has been claimed to improve soil quality, biodiversity, resource conservation, agricultural sustainability, and food security²². Although it can be strongly assumed that soil quality and biodiversity are high in permaculture systems due to permaculture design principles like „Use and Value Diversity“²³, or emphasized practices like organic mulching and no-till cultivation, there is still no scientific evidence on whole permaculture systems worldwide¹⁶.

Many practices in permaculture, such as agroforestry, crop-livestock integration, and promotion of semi-natural habitats, are also applied in agroecology and diversified farming systems, and positive environmental influences were already described in the scientific literature^{24,25}. However, agroecosystems are not just a sum of practices, but represent complex systems with many functional interactions²⁶. Permaculture takes this into account through a holistic systems design, e.g., the deliberate arrangement of context-specific land use practices and the integration of different practices, as well as management based on systems ecology and precise sustainability ethics²³. Therefore, it is essential to study whole operating farming systems to explore the full potential of permaculture. While there are numerous studies showing positive effects of isolated agroecological practices on ecosystem services^{27,28}, there is still a lack of scientific evidence on commercial farming systems with multiple integrated practices, in temperate regions, not only for permaculture but also for agroecology^{29,30}.

In this study, we investigated eight permaculture sites in Germany and one in Luxembourg from 2019 to 2021, which represent either a whole farm or part of a farm. Permaculture sites had to be designed and managed according to permaculture principles, their production had to be economically self-sufficient and at least two different land use practices (e.g., grazing and fruit trees) had to be integrated. The number and types of land use varied among permaculture sites. At each location, one field of each permaculture land use type was sampled, as well as one direct control field with locally predominant agricultural land use. We investigated soil carbon and various nutrients as chemical soil quality indicators, microbial community structure via phospholipid fatty acids (PLFAs) and earthworm abundance as biological indicators, and soil bulk density as physical indicators. With regard to biodiversity, we investigated the species richness of vascular plants as essential primary producers³¹ and the species richness of earthworms as important ecosystem engineers³². In addition, we investigated the species richness of birds as a particularly popular and widely monitored group of organisms³³. As an important habitat indicator for general biodiversity, we determined the proportion of the surveyed area with trees³⁴. In addition, interviews were conducted with farmers who manage permaculture sites to gather information on farm characteristics, as well as the usage and intentions behind permaculture practices. Several biodiversity indicators were compared with literature data from a European-wide study of ~150 conventional and organic farms³⁵. Some soil quality indicators were compared with arable land and grassland data from the first comprehensive German soil inventory³⁶.

Results

Permaculture sites showed improved soil organic carbon (Figure 1), soil quality (Figure 2, Figure 3) and biodiversity (Figure 4). Results of statistical

models are summarized in Table 3, while post hoc comparisons are displayed in Table 4. Values in the text are given as model-predicted mean \pm standard error. Concentrations of soil constituents are given per gram of soil dry matter.

Soil carbon and nutrients

We investigated soil organic carbon content in terms of concentration per gram of soil, as well as soil organic carbon stocks, which refers to the amount of carbon stored in the soil per hectare of land. On permaculture sites soil organic carbon content (3.4 ± 0.3 g 100 g⁻¹) was 71% higher compared to control fields of this study (2.0 ± 0.3 g 100 g⁻¹) as well as 94% higher than on average German arable fields (1.8 ± 0.2 g 100 g⁻¹) and by trend 18% higher than on average German grasslands (2.9 ± 0.2 g 100 g⁻¹; Fig. 1a) according to the first comprehensive soil inventory³⁶. Carbon stocks within the first 30 cm were 27% higher on permaculture sites (87 ± 9 t ha⁻¹) compared to control fields (68 ± 8 t ha⁻¹) and 37% higher than on average German arable fields (62 ± 3 t ha⁻¹; Fig. 1c)³⁶. There was no significant difference between permaculture sites and average German grasslands (90 ± 4 t ha⁻¹), indicating that permaculture is able to store similar levels of carbon as grassland while still producing a share of arable crops such as vegetables and grains. The proportion of permanent grassland among all permaculture sites was 67% (Table 2). In addition, humic topsoil was 59% deeper on permaculture sites (45 ± 4 cm) compared to control fields (28 ± 2 cm; Fig. 1b), suggesting an even higher difference in organic carbon stock. As only real agricultural land was sampled, the carbon stock values do not take into account other farmland structures such as semi-natural habitats or drive- and pathways.

Six of the nine permaculture sites studied were originally of the same land use as the direct control fields (Table 2). Assuming that carbon stocks were originally similar within pairs of site and control fields and have not changed on the control fields over the years of permaculture establishment, we can roughly estimate a level of carbon sequestration on permaculture sites of 0.82 ± 0.39 t ha⁻¹ yr⁻¹ in the first 30 cm of topsoil (Fig. 1d).

Analysis of soil nutrients, measured as plant-extractable concentrations except for nitrogen, shows a higher soil fertility on permaculture sites. Total nitrogen concentrations were 63% higher on permaculture sites (354 ± 53 mg 100 g⁻¹) compared to control fields (217 ± 33 mg 100 g⁻¹), 138% higher than on average German arable fields (148 ± 18 mg 100 g⁻¹) and 48% higher than on average German grasslands (240 ± 29 mg 100 g⁻¹; Fig. 2a). Carbon nitrogen ratios on permaculture sites (9.3 ± 0.6) were 10% higher compared to control fields and 13% and 16% lower than on average German arable fields and grasslands, respectively. Phosphorus concentrations were by trend 41% higher on permaculture sites (7.3 ± 3.1 mg 100 g⁻¹) compared to control fields (5.2 ± 2.1 mg 100 g⁻¹; Fig. 2b). Potassium concentrations were 123% higher on permaculture sites (30.6 ± 7.1 mg 100 g⁻¹) compared to control fields (13.8 ± 3.5 mg 100 g⁻¹; Fig. 2c) and Magnesium concentrations were 66% higher on permaculture sites (17.5 ± 2.4 mg 100 g⁻¹) compared to control fields (10.5 ± 1.6 mg 100 g⁻¹; Fig. 2d).

Some soil micronutrient levels were also increased under permaculture. Boron concentration was 51% higher on permaculture sites (0.56 ± 0.13 mg g⁻¹ versus 0.37 ± 0.09 mg g⁻¹; Fig. 2e), and zinc concentration on permaculture sites was 80% higher compared to control fields (7.6 ± 1.5 mg g⁻¹ versus 4.2 ± 0.9 mg g⁻¹; Fig. 2f). We did not find significant differences in soil copper and manganese levels.

Soil pH was not significantly different between permaculture sites with 6.2 ± 0.2 and control fields with 6.2 ± 0.2 .

Soil physics and biology

We investigated the soil bulk density as an indicator of soil compaction and erosion potential. In the deeper topsoil (10–30 cm) soil bulk density on permaculture sites was 20% lower on permaculture sites (1.08 ± 0.05 g cm⁻³) compared to control fields (1.36 ± 0.05 g cm⁻³) and 24% and 20% lower than on average German arable fields (1.43 ± 0.03 g cm⁻³) and grasslands (1.35 ± 0.03 g cm⁻³; Fig. 3a),

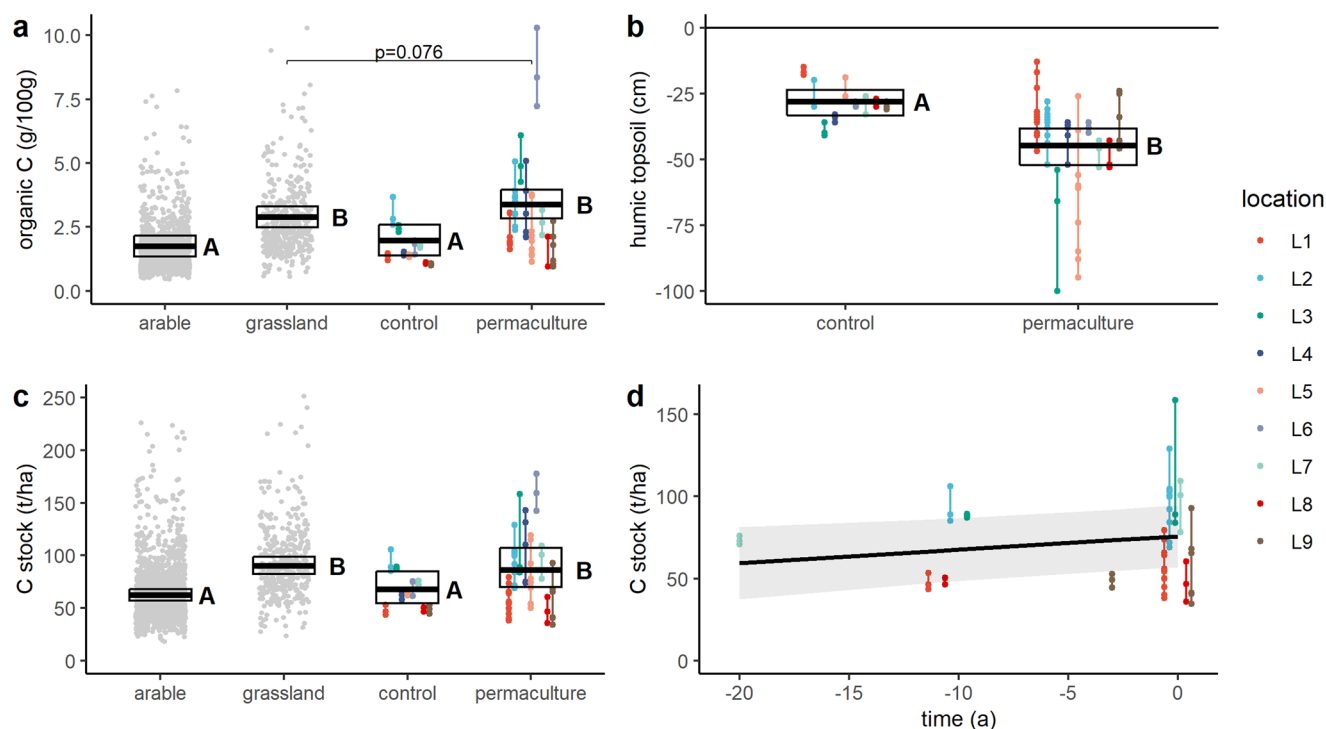


Fig. 1 | Soil organic carbon. **a** Topsoil (30 cm) organic carbon content on nine permaculture sites, direct control fields of locally predominant agriculture and German grassland ($n = 387$) and arable land ($n = 1683$)³⁶. **b** Humic topsoil depth on nine permaculture sites and direct control fields of locally predominant agriculture. **c** Topsoil (30 cm) organic carbon stock on nine permaculture sites, direct control fields of locally predominant agriculture and German grassland ($n = 387$) and arable land ($n = 1683$)³⁶. **d** Roughly estimated topsoil (30 cm) carbon sequestration ($p = 0.044$, $\chi^2 = 5.05$, $df = 52$) on six permaculture sites under the assumption that

carbon level was originally sufficiently equal on site pairs and did not change on control fields. To set today as a baseline, the age of the permaculture sites was set to zero, and the age of the paired control sites was set to the negative age of the corresponding permaculture site. Here, the black line indicates a significant linear regression slope and 95% confidence interval. Dots indicate individual data points. Colors indicate sampling pair locations and gray dots indicate data points of literature data. Crossbars indicate the model-predicted mean and 95% confidence interval. Treatments not sharing the same letters are significantly different.

respectively³⁶. Gravimetric soil water content at sampling was significantly higher on permaculture sites with $31 \pm 4\%$ compared to control fields with $21 \pm 3\%$, while there was only a by trend increase in volumetric soil water content ($30 \pm 4\%$ versus $27 \pm 3\%$).

As macrofaunal indicator of soil quality, we found a 201% higher earthworm abundance on permaculture sites ($153 \pm 57 \text{ m}^{-2}$) compared to control fields ($51 \pm 21 \text{ m}^{-2}$) and a 205% and 331% higher abundance compared to average European organic ($50 \pm 7 \text{ m}^{-2}$) and conventional farms ($36 \pm 5 \text{ m}^{-2}$; Fig. 3b), respectively³⁵.

To evaluate soil microbiology, we determined PLFA in upper topsoil samples (0–10 cm). As indicator for microbial biomass, we found 42% higher total PLFA concentrations on permaculture sites ($7.6 \pm 1.5 \text{ nmol g}^{-1}$) compared to control fields ($4.2 \pm 0.9 \text{ nmol g}^{-1}$; Fig. 3c). On permaculture sites, concentrations of bacteria PLFA were 56% higher ($5.5 \pm 1.1 \text{ nmol g}^{-1}$ versus $3.5 \pm 0.7 \text{ nmol g}^{-1}$) and concentrations of fungi PLFA were 86% higher ($0.9 \pm 0.3 \text{ nmol g}^{-1}$ versus $0.5 \pm 0.2 \text{ nmol g}^{-1}$). We found a trend to higher ratio of gram-positive to gram-negative bacteria PLFA on permaculture sites with 0.12 ± 0.03 compared to 0.09 ± 0.03 . We found no differences in the ratio of fungi to bacteria PLFA and the ratio of arbuscular mycorrhizal to saprophytic fungi PLFA between permaculture sites and control fields.

Biodiversity

We investigated the species richness of vascular plants and earthworms to focus on management effects and minimize the impact of landscape effects that are common in more mobile organisms. Vascular plant species richness was 457% higher on permaculture sites (36 ± 6 species) than on control fields (6 ± 2 species) and 190% and 200% higher than on European organic (19 ± 1) or conventional farms (18 ± 1 ; Fig. 4a), respectively³⁵. Earthworm species richness was by trend 77% higher on permaculture sites

(3.3 ± 0.7 species) as on control fields (1.9 ± 0.7 species), while there was no significant difference to other European farms (Fig. 4b)³⁵. We also found that bird species richness was 197% higher on permaculture sites (3.6 ± 1.2 species) than on control fields (1.2 ± 0.5 species; Fig. 4c).

As a habitat indicator for biodiversity, the proportion of agricultural area surveyed with trees was higher on permaculture sites with $75 \pm 13\%$ compared to European organic farms with $29 \pm 4\%$ and conventional farms with $29 \pm 3\%$ (Fig. 4d)³⁵. This farm-level indicator is not compared to control fields, which in any case contained no trees.

Farm characteristics

The farms utilizing permaculture were, on average, 11 ± 5 years old and had an average area of 13.8 ± 8.4 ha (Table 2). Eight out of nine investigated farms had an area of <20 ha, while only 45% of all farms in Germany fall into this category³⁷. Permaculture sites amounted to a mean of 2.8 ± 1.0 ha and were thus clearly smaller than the areas of the farms they belong to. In addition, other sources of income such as non-permaculture agriculture and seminars, many farms provided land for semi-natural habitats to foster ecosystem services and nature conservation. All farms utilizing permaculture were involved in some form of direct marketing, mostly through farm shops, community-supported agriculture, vegetable box delivery, or supply of gastronomy. All permaculture farms work according to the guidelines of organic agriculture, but not always with certification.

The main permaculture practices applied by the study farms can be grouped into three general categories (Table 1). The first category is the integration of land use elements to create synergies and strengthen the resilience and stability of the agroecosystem. Agroforestry has mainly been applied as a combination of fruit trees with grazing livestock or vegetable production. Crop-livestock integration was also practised as intermitted grazing of vegetable or cereal fields by pigs or chickens.

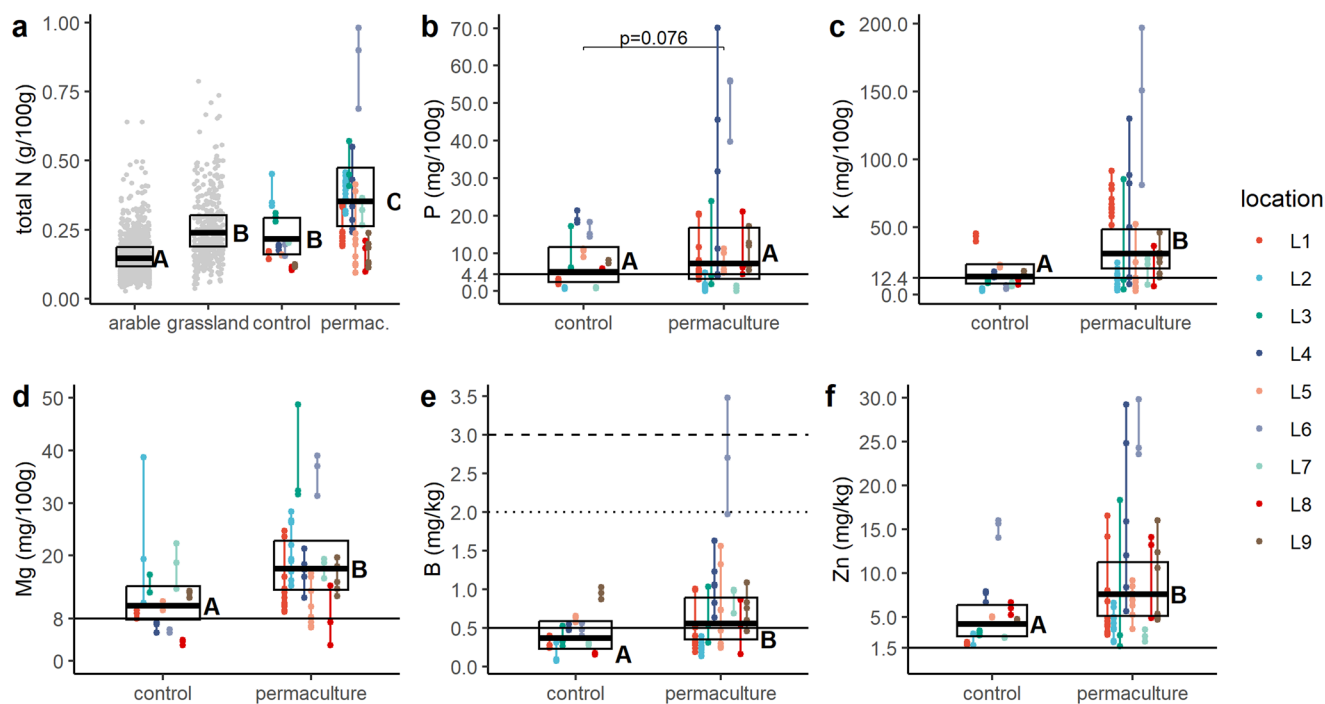


Fig. 2 | Soil macro- and micronutrients. **a** Topsoil (30 cm) total nitrogen content on nine permaculture sites, direct control fields of locally predominant agriculture and German grassland ($n = 387$) and arable land ($n = 1683$)³⁶. Topsoil (30 cm) plant available phosphorus (**b**), potassium (**c**), magnesium (**d**), boron (**e**), and zinc (**f**) concentrations on nine permaculture sites and direct control fields of locally predominant agriculture. **b–d** solid line indicates lowest aspirational concentration in soils with medium soil texture in Germany³⁷. **e** Solid line represents soil boron plant

deficiency level^{38,39} and dotted and dashed lines represent different suggested soil boron plant toxicity thresholds^{38,40}. **f** Solid line represents soil zinc plant deficiency level^{41,42}. Dots indicate individual data points. Colors indicate sampling pair locations. Crossbars indicate model-predicted mean and 95% confidence interval. Treatments not sharing the same letters are significantly different. Non-significant p values < 0.1 are written in the plot.

The second category is the promotion of biodiversity for the provisioning of ecosystem services. An important part of permaculture cultivation has been the utilization of semi-natural habitats to increase pollination and pest control, such as wildflower strips, ponds, more specialized habitats to support reptiles or amphibians, and extensively managed grassland.

The third category is the restoration of soil fertility, where manual labor is preferred over mechanized work in vegetable production. Market Gardening or bio-intensive mini-farming with dense and highly diverse crop cultures, a high degree of manual labor, minimum tillage, and permanent soil cover with straw or compost was mainly used for vegetable production. Similar to that, Hugelkultur, an extensive version of high permanent raised beds with a core of organic material, was used to further improve soil fertility, mitigate the effects of waterlogging, and recycle organic waste generated on the farm. A variation of holistic grazing management, which mimics the pattern of densely packed and constantly moving herds of wild grazing animals, was implemented with laying hens to improve soil and grassland quality.

However, it should be stressed that permaculture should not be reduced to a specific set of practices but also involves the conscious arrangement of context-specific land use practices and general management based on precise sustainability ethics.

Discussion

The results of this study highlight that permaculture in Central Europe enables higher carbon stocks, soil quality and biodiversity compared to predominant agriculture. Soil carbon stocks in the first 30 cm of topsoil on permaculture sites were comparable to average German grasslands while still producing cereals, vegetables, and fruit. In Germany, grasslands have on average a higher organic carbon content in the topsoil than even forests³⁸. Deeper humic topsoil layers on permaculture sites indicate that the increase in total soil organic carbon exceeds the difference in carbon stocks observed in the first 30 cm of soil. Our estimate shows that

permaculture with a mean soil carbon sequestration of $0.8 \text{ t ha}^{-1} \text{ year}^{-1}$ could exceed the average sequestration rate of $0.6 \text{ t ha}^{-1} \text{ year}^{-1}$ proposed by the “4 per 1000” initiative launched as a result of the 2015 United Nations Climate Change Conference⁵. While this estimate depends on assumptions, it may still be underestimated as the higher depth of humic topsoil on permaculture sites was not taken into account. In contrast, average net carbon losses have been observed for the predominant industrial agriculture in the past³⁹ and are predicted for the future⁴⁰. We assume that the increased carbon stocks on permaculture sites are the result of a combination of various different practices. The carbon input is increased by the application of organic matter in the form of compost, livestock manure, organic mulch, or terra preta⁴¹. Here, it should be noted that overall carbon sequestration may be lower if part of this organic matter originates from outside the permaculture site and would otherwise have been stored in soils elsewhere. Carbon losses due to CO_2 emissions and topsoil erosion were not investigated in this study but are likely to be reduced in permaculture through permanent soil cover, reduced or no tillage, agroforestry, and decreased soil compaction⁴².

We also found higher total nitrogen contents on permaculture sites. On the one hand, higher nitrogen contents promote plant productivity, but on the other hand, this means an increased risk of gaseous losses, e.g., nitrous oxide or ammonia into the atmosphere or nitrate leaching into groundwater⁴³. As permaculture farms work with minimal or no tillage, permanent soil cover, and without mineral nitrogen fertilizers, it can be assumed that the risk of nitrogen losses is low⁴³. A higher C/N ratio on permaculture sites is a limiting factor for the mineralization rate of nitrogen from organic inputs, while higher carbon and nitrogen levels, as well as higher microbial biomass, facilitate mineralization⁴⁴. There was a trend towards a higher ratio of Gram-positive to Gram-negative bacteria on permaculture sites, indicating a higher proportion of more complex and recalcitrant carbon sources from soil organic matter⁴⁵. However, as the nitrogen and carbon cycles in soil are complex, more detailed investigations

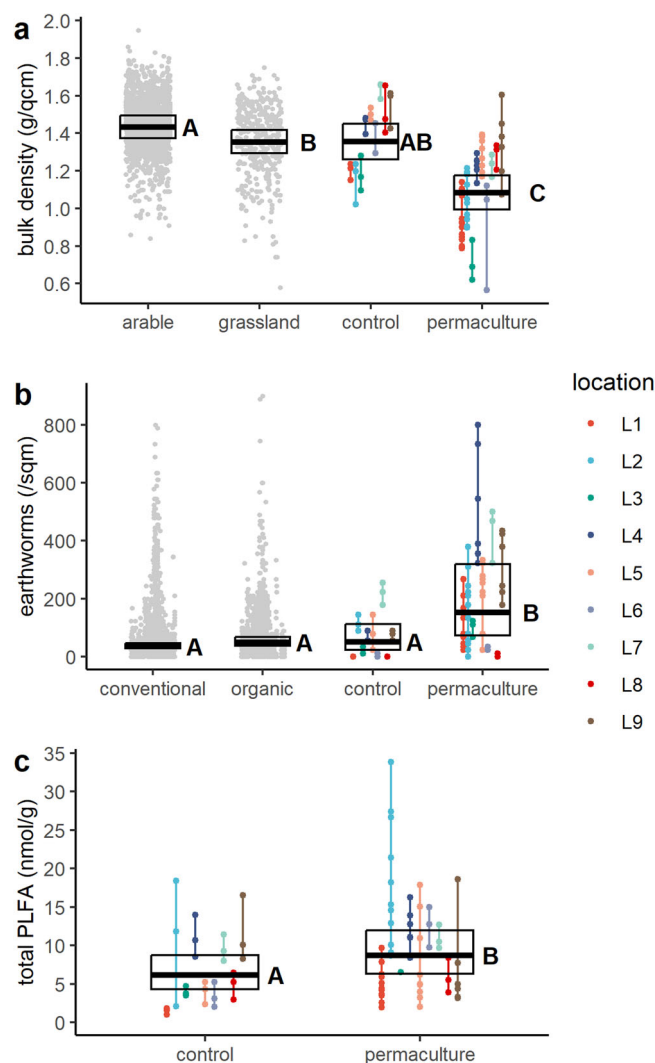


Fig. 3 | Soil biological and physical parameters. **a** Soil bulk density at 10–30 cm depth on nine permaculture sites, direct control fields of locally predominant agriculture and German grassland ($n = 387$) and arable land ($n = 1683$)³⁶. **b** Earthworm abundance in the top 20 cm on nine permaculture sites, direct control fields of locally predominant agriculture, and European organic ($n = 60$) and conventional ($n = 77$) farms³⁵. **c** Total microbial phospholipid fatty acid concentration in the top 10 cm on nine permaculture sites and direct control fields of locally predominant agriculture. Dots indicate individual data points. Colors indicate sampling pair locations and gray dots indicate data points of literature data. Crossbars indicate the model-predicted mean and 95% confidence interval. Treatments not sharing any same letters are significantly different.

are needed to make reliable statements on actual dynamics in and possible losses from permaculture sites.

The plant-extractable concentrations of soil phosphorous, potassium, magnesium, boron, and zinc were higher on permaculture sites than on conventionally fertilized soils of the control fields, which can be explained by a higher input of organic matter. These increases, which lead to improved contents with regard to plant deficiency thresholds (Fig. 3), indicate a higher soil quality in terms of plant nutrient supply. This is particularly important for phosphorous, as the permaculture sites worked according to organic farming standards and were, therefore, able to achieve high soil fertility without applying limited mineral resources. Still, one permaculture site with possibly plant-toxic soil boron levels suggests that organic nutrient inputs should also be handled with caution. Higher plant-extractable soil zinc concentrations, leading to increased contents in crops, are important to combat widespread zinc malnutrition in humans⁴⁶. In line with our results, a case study on a permaculture farm in France found higher concentrations of

soil carbon and bioavailable nutrients compared to pasture and arable agriculture⁴⁷.

A high input of organic matter together with minimal or no tillage is probably responsible for lower soil bulk densities^{48,49} and increased abundances and diversity of earthworms on permaculture sites⁵⁰. Soil bulk density is a key soil quality indicator with respect to plant root penetration, aeration, and infiltration and hereby codetermines erosion potential^{51,52}. An increased earthworm abundance facilitates a reduced soil bulk density and vice versa⁵³. Earthworms improve soil nutrient cycling, structural stability, and soil porosity, reduce run-off^{32,50}, and can even suppress crop pathogens^{54,55}. A recent meta-analysis has shown that earthworms substantially increase crop yield by releasing nitrogen from organic matter, making them crucial for farmers who do not use mineral nitrogen fertilizers⁵⁶. Mineral nitrogen fertilization directly promotes methane and nitrous oxide emissions from the soil, and the corresponding production process is one of the main contributors to greenhouse gas emissions from the agricultural system⁵⁷. Earthworms are proposed as key indicators of soil biodiversity⁵⁰, which is recognized by both the Convention on Biological Diversity⁵⁸ and the European Commission⁵⁹ as essential for ecosystem functioning and the provision of soil services to humans.

Greater plant diversity increases rhizosphere carbon inputs to the microbial community leading to an increased microbial biomass and activity as well as soil carbon stocks, both of which have been found on permaculture sites⁶⁰. More diverse vegetation also favors earthworms by providing nutritionally higher-quality root-derived carbon resources^{61,62}. Vascular plants are the essential primary producers in agricultural systems, as well as a key resource for functionally important taxa of pollinators and natural pest enemies³¹. Avoiding the use of herbicides, focusing on mixed cropping, integrating herbaceous and woody crops, and small-scale cultivated areas could be the reasons for the strong increase in plant diversity on permaculture sites. Vascular plant diversity has been shown to be a good indicator of overall biodiversity⁶³, and there is consistently strong evidence that strategically increasing plant diversity increases crop and forage yield, yield stability, pollinators, weed suppression, and pest suppression⁶⁴. We also found a substantially higher proportion of the land with trees on permaculture sites. Trees are an effective habitat indicator for overall species richness in agricultural landscapes³⁴ while increasing the abundance of pollinators and natural enemies⁶⁵. Establishing trees is also one of the most important climate change mitigation measures on agricultural land⁶⁶ and could also mitigate other negative impacts of the conversion of forest biomes to agricultural land in the past and present¹. The increases in plant species richness and tree habitats could be an explanation for the higher bird species richness on permaculture sites, as farmland bird biodiversity is closely related to semi-natural habitats⁶³. Apart from their great importance as a flagship group for biodiversity conservation, farmland birds play an important role in insect pest control and weed suppression but are also responsible for potential crop damage⁶⁷.

Variability and land use history of permaculture sites

The variance of some variables assessed on permaculture sites was much higher compared to control sites. As permaculture is a very context-specific design tool, the differences between permaculture systems can be high. We assume that the variance between permaculture sites is the result of a combination of different factors, such as the degree of complexity, the intensity of land use, the level of implementation of permaculture principles, and the experience of the farmers. The degree of complexity varied between permaculture sites, for example, in the level of spatial and temporal integration of different land use practices, from mixed culture of vegetables to agroforestry and the integration of different types of livestock.

Given that the previous land use on the permaculture sites was, in most cases, similar to the land use on the control fields, it is unlikely that the land use history significantly contributes to the observed differences in biodiversity, soil quality, and carbon stocks. In three out of nine permaculture sites, part of the area had a history of grassland use. This may have contributed to the improved soil quality parameters compared to an arable

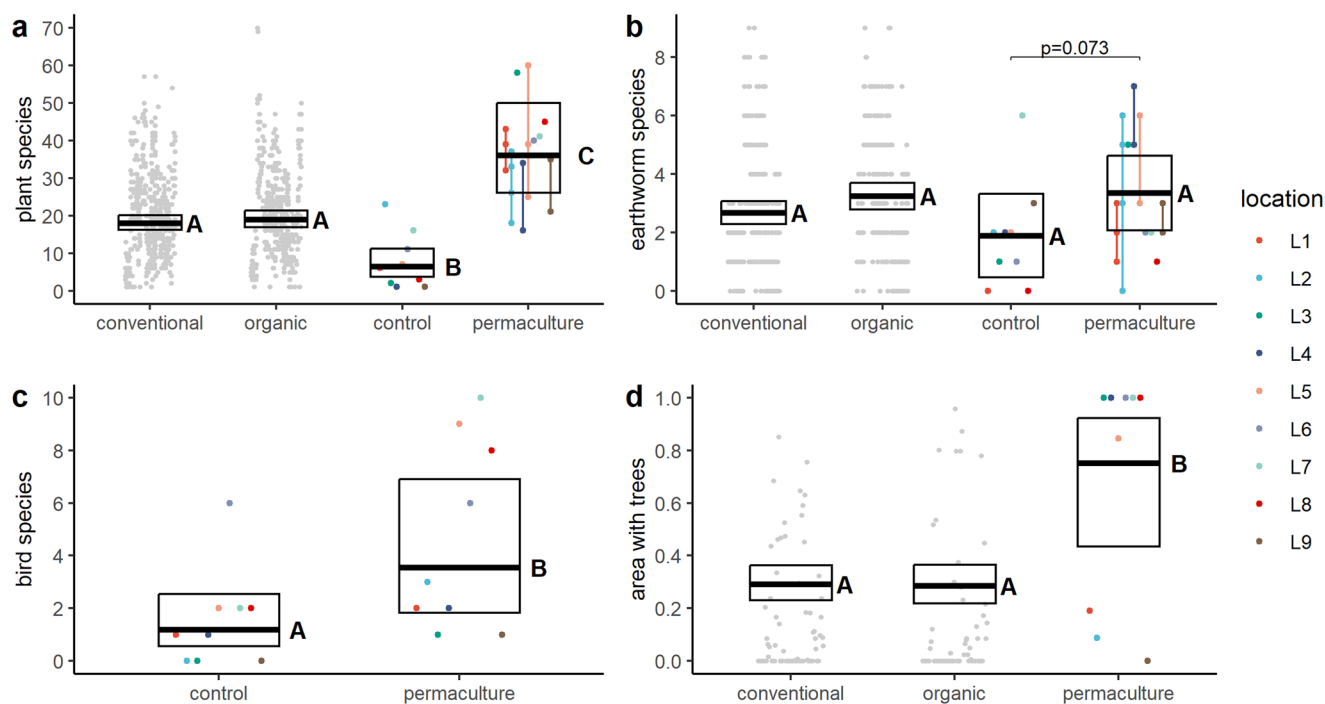


Fig. 4 | Biodiversity indicators. **a** Vascular plant species richness on 100 m² for nine permaculture sites, direct control fields of locally predominant agriculture and European organic ($n = 68$) and conventional ($n = 79$) farms³⁵. **b** Earthworm species richness on 0.27 m² for nine permaculture sites, direct control fields of locally predominant agriculture, and European organic ($n = 60$) and conventional ($n = 77$) farms³⁵. **c** Bird species richness based on songs recorded within around 70 m from the middle of nine permaculture sites and direct control fields of locally predominant

agriculture. **d** Proportion of area with trees on nine permaculture sites and European organic ($n = 68$) and conventional ($n = 79$) farms³⁵. This farm-level indicator is not compared to control fields that did not include trees in any case. Dots indicate individual data points. Colors indicate sampling pair locations and gray dots indicate data points of literature data. Crossbars indicate model-predicted mean and 95% confidence interval. Treatments not sharing the same letters are significantly different. Non-significant p values < 0.1 are written in the plot.

control field. However, it is more likely that other factors related to the permaculture practices and management itself are responsible for the observed differences, as the results for most assessed parameters were consistent at all permaculture sites. In contrast, different land use histories may have contributed to the high variance between permaculture sites.

Comparison with individual practices

We found that permaculture farms in Germany and Luxembourg tend to be rather small and young, which is similar to US permaculture farms⁶⁸. Small farm sizes are favored by a low level of mechanization in combination with recent farm establishment⁶⁸. The permaculture farms in this study relied exclusively on some form of direct marketing model. This reflects a higher level of consumer integration in food production and the possibility of obtaining sufficiently high prices for agricultural products. Permaculture

farmers applied various practices to promote agroecosystem self-regulation by increasing carbon stocks, soil quality and biodiversity (Table 1). Our findings clearly show that permaculture farmers' intentions to change crucial ecosystem properties are successful. The most common practices applied on permaculture sites in this study were agroforestry, crop-livestock integration, market gardening, and facilitation of semi-natural habitats (Table 1). These practices are also associated with agroecology^{24,25}. As there are no studies on whole commercial farms and temperate regions for agroecology³⁰, the most important variables are discussed in relation to agroforestry, crop-livestock integration, and facilitation of semi-natural habitats. As there are few studies on market gardening⁶⁹, the application of compost mulch is discussed as one of its key elements⁷⁰.

Permaculture sites had 27% higher soil carbon stocks and 71% higher soil carbon content. A meta-analysis found that carbon stocks are 19% higher in agroforestry systems worldwide, with the increase being slightly higher in subtropical climates than in temperate and tropical climates⁷¹. Soil organic carbon stocks in the top 30 cm of soil were 1% to 8% higher on four silvoarable agroforestry systems compared to control plots in France⁷². Soil carbon content was 27% higher for integrated crop-livestock versus only crop systems in Texas, USA⁷³. No differences in soil carbon content were found between only crop and only pasture systems versus crop-livestock integration in Illinois, USA⁷⁴, nor in soil carbon stocks between only crop versus crop-livestock integration in the Pampas of Argentina⁷⁵. It is difficult to estimate the effect of integrating semi-natural habitats into agricultural areas on soil carbon, especially when semi-natural habitats are not directly measured, as in this study. However, a review found a positive effect of semi-natural habitats on soil carbon in 17 out of 19 studies⁷⁶. A global meta-analysis on land use change found that soil organic carbon stocks increase by 19% when cropland is converted to pasture and by 54% when cropland is converted to secondary forest⁷⁷. Repeated application of compost mulch was found to increase soil carbon content by ~40% to 120%^{78–80}.

Table 1 | Summary of main permaculture practices utilized on permaculture sites in this study

| Permaculture practice | Number of farms | Farms [ID] |
|----------------------------------|-----------------|--------------------------------|
| Agroforestry | 8 | L1, L2, L3, L4, L5, L6, L7, L8 |
| Crop-livestock integration | 6 | L1, L2, L4, L5, L7, L9 |
| Market gardening | 6 | L1, L2, L4, L6, L8, L9 |
| Wildflower strips | 6 | L1, L2, L4, L5, L6, L8 |
| Ponds | 5 | L1, L2, L3, L5, L6 |
| Additional semi-natural habitats | 5 | L2, L3, L5, L6, L8 |
| Extensive grassland management | 3 | L1, L2, L7 |
| Holistic grazing management | 2 | L4, L9 |
| Hugelkultur | 2 | L3, L5 |

In this study, permaculture sites were found to have 20% lower soil bulk density. No significant difference in soil bulk density was found on six silvoarable and silvopastoral agroforestry sites compared to control plots in France⁷². A 1% lower soil bulk density was found on silvopastoral and agrosilvopastoral systems compared to continuous cropping in semi-arid climate in Brazil⁸¹. A 7% increase in soil bulk density was found both for crop-livestock integration in perennial pasture and in arable crop rotation compared to continuous cropping in Texas, USA⁸². In Georgia, USA, no effect of crop-livestock integration on soil bulk density was found for different tillage treatments⁸³. Also, no difference in soil bulk density was found between semi-natural grasslands and apple orchards in Belgium⁸⁴ and between semi-natural habitats and field margins in Ontario, Canada⁸⁵. In contrast, repeated application of compost mulch on agricultural soils reduced soil bulk density by 13% in California, USA⁸⁶, and by 9% in Wisconsin, USA⁸⁷.

Plant species richness was 457% higher on permaculture sites than on control fields. Two meta-analyses on European agroforestry systems found no significant effect on plant biodiversity^{88,89}. There are no clear results on the effect of crop-livestock integration on plant species richness. However, the integration of livestock in a cover crop and soybean rotation in Rio Grande do Sul, Brazil, led to an increase in weed species richness by ~110%⁹⁰. The proportion of semi-natural habitats on farmland had no effect on plant species richness in France⁹¹. In contrast, a global meta-analysis showed, that ecological restoration, often through the facilitation of semi-natural habitats, increased plant biodiversity by ~60%⁹². Compost application on grasslands in California, USA, had no effect on plant species richness⁹³.

Taken together, the results on isolated agroecological practices do not fully explain the strong effects of permaculture on carbon stocks, soil quality and biodiversity found in this study. The holistic systems approach of permaculture takes into account the interconnections and interdependencies between various elements of an agroecosystem^{17,23}, which could explain the advantages over isolated practices⁹⁴. Complementary effects could compensate for the limitations or trade-offs of individual practices⁹⁵, while additive or even synergistic effects may explain a stronger response compared to individual practices⁹⁶. In addition, the combination of various different practices might also increase the resilience and adaptability of the agricultural system⁹⁷.

Conclusion

In this study, we observed strong increases in soil carbon stocks, soil quality, and biodiversity through the use of permaculture. These results suggest that permaculture could contribute to the urgently needed transformation of agriculture to mitigate negative effects on various Earth system processes such as climate change, biogeochemical nitrogen and phosphorous flows, biosphere integrity, land-system change, and soil degradation^{98,99}. Our results suggest that permaculture is an effective tool to promote sustainable agriculture (SDG 2), ensure sustainable production patterns (SDG 12), combat climate change (SDG 13) and halt and reverse land degradation and biodiversity loss (SDG 15)¹⁰⁰. While there are numerous scientific results on more environmentally friendly practices such as agroforestry, crop-livestock integration, or the promotion of semi-natural habitats, the key capability of permaculture is to select, combine, and arrange precise practices for a specific context of land and farmer to create synergistic, regenerative and resilient agroecosystems. We see this as the missing link between scientific knowledge and implementation in practice. Therefore, we propose to foster the education of farmers and specialized consultants in permaculture design and related practices, as well as the redesign of agricultural systems according to permaculture principles. As the number of permaculture sites we were able to evaluate was still small and the variance between them was high, we also suggest further research on larger numbers of permaculture sites in different climates to provide evidence on more detailed processes. We are suggesting four major research questions: First, which variables, such as adopted practices, land use type(s), system complexity, crop productivity, and level of mechanization, determine the environmental effects of permaculture, and to which extent? Second, how strong are the

synergistic or interactive effects of multiple integrated practices and land use types? Third, what are the pathways of nutrients and organic carbon, to, on, and from permaculture sites? And finally, what is the crop yield potential of permaculture systems in comparison to predominant industrial agriculture? We hope that answering these questions can promote wider adoption of permaculture and agroecology, enabling future agriculture to enhance its sustainability.

Materials and methods

Study sites

The study was conducted in Germany and Luxembourg in 2019, 2020, and 2021. In this area, nine permaculture sites were selected, constituting either a whole farm or part of a farm. Three criteria were used for selection. First, permaculture sites had to be designed and managed with permaculture, according to the farmer. Second, this agroecological production had to pay for itself, not being financed by other incomes of the farm. Third, at least two different land use practices had to be integrated into the agroecological production, either in the same area (e.g., tree crops and vegetables), temporally (e.g., livestock on crop areas), or indirectly (e.g., transfer of biomass). This criterion was included to recognize the principle of permaculture on creating synergies through the integration of various land use practices. We included all permaculture sites we could find that fit our criteria and were willing to participate. Due to the Covid-19 pandemic, we were limited to Germany starting from 2020.

At each permaculture site, one field of each land use type (e.g., vegetables, arable crops, tree crops, grassland, grazed land) was randomly selected to be sampled (called sampling plot). Permaculture sites with corresponding land use types, determining the number of sampling plots for each permaculture site, are listed in Table 2. Minimum area for individual field elements to be considered for sampling was 400 m² to fit the selection procedure of the study, whose data we used for comparison^{35,101}. Areas of field elements were determined using QGIS 3.28.2. Only true agricultural areas were measured, all pathways broader than 30 cm (small footpaths between vegetable beds) were excluded. For each permaculture site, one control field with a locally predominant agricultural land use type was selected no further than three kilometers to ensure comparable climatic and geological conditions. In most cases, land use of control fields equaled previous land use on permaculture sites (Table 2). Locally predominant agricultural land use type was determined based on farmers interviews and supported by evaluation of aerial images five kilometers around the permaculture site using QGIS 3.28.2. Land use history of permaculture sites is reported in Table 2 and equalled land use of control fields for six out of nine cases.

Sampling was done between mid of May and beginning of June to ensure enough moisture for earthworm sampling as well as sufficient vegetation development for assessment of plant diversity. Each sampling was done within the same two days for each pair of permaculture site and control field.

Interview of farmers

Farmers were asked about farm area, permaculture site age, marketing strategies of agricultural produce, additional incomes, if working according to guidelines of organic agriculture (with or without certification), and which permaculture practices they use and why. Farmers of both permaculture sites and control fields were asked about predominant regional agricultural land use type and land use history of sampled fields (Table 2).

Soil sampling

At each sampling plot, soil samples were taken at three sampling points, being 10 m apart from each other and 20 m from the border of the field, if possible. In the case of raised beds or Hugelkultur, one sample each was taken from the center of the bed, the border to a footpath separating beds and the middle in between. At each sampling point, samples were taken from two depths, 0–10 cm, and 10–30 cm. The soil samples of 0–10 cm depth were stored at 6 °C, a subsample was freeze-dried within 24 hours for at least 36 hours and stored at –20 °C for later analysis of PLFA. At each

Table 2 | Characteristics of investigated permaculture (PC) sites

| location ID | farm area [ha] | PC site area [ha] | PC site age [a] | Land use type | Area [ha] | Detail | Previous land use | Control field |
|-------------|----------------|-------------------|-----------------|---------------|-----------|---------------------------------------|--------------------|----------------------------------|
| L1 | 14 | 10.4 | 11 | arable | 2.0 | fodder crops | arable (>30 a) | wheat (arable, >50 a) |
| | | | | grassland | 1.8 | laying hens, hay production | arable (>30 a) | |
| | | | | grazing | 5.7 | sheep, cattle, fruit trees | arable (>30 a) | |
| | | | | vegetables | 0.9 | vegetables | arable (>30 a) | |
| L2 | 10 | 1.7 | 10 | arable | 0.9 | pigs, grains, fodder crops | grassland (>50 a) | mowing meadow (grassland, >50 a) |
| | | | | grassland | 0.5 | hay production | grassland (>50 a) | |
| | | | | grazing | 0.1 | geese, fruit trees | grassland (>50 a) | |
| | | | | vegetables | 0.2 | vegetables | grassland (>50 a) | |
| L3 | 3.6 | 0.8 | 10 | vegetables | 0.8 | vegetables, fruit trees | arable (>10 a) | wheat (arable, >20 a) |
| L4 | 2.5 | 0.9 | 4 | grazing | 0.7 | laying hens, fruit trees | Streuobst (>15 a) | wheat (arable, >20 a) |
| | | | | vegetables | 0.2 | vegetables, fruit trees, berry bushes | arable (>15 a) | |
| L5 | 10 | 3.1 | 8 | arable | 0.4 | pigs, root crops | industrial (>50 a) | fodder beet (arable, >50 a) |
| | | | | grazing | 2.6 | sheep, fruit trees | grassland (>10 a) | |
| | | | | vegetables | 0.1 | vegetables | industrial (>50 a) | |
| L6 | 1.5 | 1.0 | 5 | vegetables | 1.0 | vegetables, fruit trees, berry bushes | Streuobst (>10 a) | vegetables (vegetables, >50 a) |
| L7 | 80 | 2.6 | 20 | grazing | 2.6 | cattle, fruit trees | grassland (>10 a) | hayfield (grassland, >50 a) |
| L8 | 1 | 0.9 | 11 | vegetables | 0.9 | vegetables, fruit trees, berry bushes | arable (>10 a) | wheat (arable, >50 a) |
| L9 | 2 | 1.8 | 3 | grazing | 1.4 | laying hens | arable (>20 a) | wheat (arable, >20 a) |
| | | | | vegetables | 0.4 | vegetables | arable (>20 a) | |

Land use history of control fields is given in parentheses.

sampling point an undisturbed soil sample was taken with a soil sampling ring ($d = 5$ cm, $h = 5$ cm) from the middle of each sampling depth (ca. 5 and 20 cm) to determine soil bulk density and water content. Therefore samples were stored airtight, weighted in field-wet condition, dried at 95 °C for at least 24 hours, and weighted again.

At each sampling point the depth of the humic topsoil layer was determined with a „Pürckhauer“ soil sampler up to 1 m deep. Depths of >1 m were taken as 1 m for data analysis.

Earthworm sampling

At each soil sampling point a soil core of 30 cm × 30 cm × 20 cm deep was taken out and hand sorted for earthworms for 20 minutes by one person. This sampling procedure was based on the approach of ref. 35, to allow for comparability with this dataset. In contrast to the approach of ref. 35 no extraction solution was applied to the ground. Earthworms were preserved in 70% ethanol for later determination in the lab. Earthworms were determined to species level, if possible.

Vegetation sampling

At each sampling plot, a square plot of 100 m² was set up with a distance of at least 20 m from the borders of the field, if possible. All vascular plants within the square plot were determined to species level, to determine species richness. It was recorded if the tree cover of the sampling plot was higher than 1%. This sampling procedure was based on the approach of ref. 35, to allow for comparability with this dataset.

Bird recording

At each permaculture site and control field, one audio recorder (Audio-Moth) was deployed. The audio recorders were positioned in the middle of the site area or control field and at similar distances (at least 80 m) to natural habitats (tree rows, hedges, forests) for each pair of farm and control fields. Bird calls were recorded three times for 10 minutes each: around sunrise, one hour after sunrise, and around sunset¹⁰². For each pair of farm and

control fields, bird calls were recorded on the same day. Sampling days were selected according to weather conditions (no rain, no strong wind).

All audio recordings were resampled at 22,050 Hz in order to improve frequency resolution¹⁰³. In each recording all species present were identified aurally and visually. With the help of the software Audacity (version 5.4.8), a 1024-point Hann window spectrogram showed frequency variations over time. Species identifications were verified using the databases Xeno-canto (xeno-canto.org), e-bird (ebird.org), and Tierstimmenarchiv (tierstimmenarchiv.de). Songs or calls that could not be identified to species level were not included in further analysis. For each bird individual the maximal relative should level was measured in decibels (dB) and its associated frequency in Hertz (Hz) using the software Kaleidoscope Pro (version 5.4.8). The maximal relative sound level was measured by selecting the area around the loudest song or call in the recording. It was used as an indicator for the distance of the respective bird individuals from the recorder¹⁰⁴. To exclude birds located outside the permaculture site, only songs or calls above −35 dB were included, since this loudness is typically shown by species singing no further than 70 m of the recorder (Manon Edo, unpublished data).

Soil analysis

Soil laboratory analysis was done by the Agricultural Research Institute Speyer, Germany (LUF A Speyer). Extraction and analysis procedure followed the methods in the manual of the Association of German Agricultural Research Institutes (VDLUF A)¹⁰⁵. In the following, corresponding chapters with detailed approaches are given in parentheses.

Soil pH was determined by electrometric measurement of H⁺ ion activity in CaCl₂ solution (A 5.1.1). Dumas combustion method was used to determine soil organic carbon (A 4.1.3.1) and total nitrogen (A 2.2.5). Phosphate and potassium oxide were extracted with calcium-acetate-lactate solution (CAL) and determined by photometric measurement (A 6.2.1.1). Magnesium was extracted with calcium chloride solution and measured with optical emission spectrometry (ICP-OES) (A 6.2.4.1). Boron, copper, manganese, and zinc were extracted with calcium chloride and DTPA

Table 3 | Results of statistical evaluation of each response variable

| Response variable | Distribution family | Explanatory variable (fixed) | χ^2 value | Residual df | <i>p</i> value | Random factors |
|------------------------------|---------------------|------------------------------|----------------|-------------|------------------|-----------------------------|
| Bird species richness | genpois | management | 14.10 | 14 | <0.001 | location |
| Earthworm abundance | nbinom1 | management | 40.80 | 2267 | <0.001 | location |
| Earthworm species richness | gaussian | management | 9.30 | 759 | 0.026 | location |
| Plant species richness | genpois | management | 52.38 | 843 | <0.001 | location |
| Tree area | ordbeta | management | 8.47 | 149 | 0.014 | location |
| pH-value | gaussian | management | 0.36 | 80 | 0.55 | location, texture class |
| Gravimetric moisture | ordbeta | management | 42.89 | 77 | <0.001 | location, texture class |
| Volumetric moisture | ordbeta | management | 3.42 | 77 | 0.064 | location, texture class |
| Humic topsoil depth | nbinom2 | management | 48.81 | 79 | <0.001 | location, texture class |
| Bulk density | gaussian | management | 244.7 | 2147 | <0.001 | location, texture class |
| Organic C content | gaussian | management | 506.5 | 2147 | <0.001 | location, texture class |
| Organic C stock | nbinom2 | management | 355.4 | 2147 | <0.001 | location, texture class |
| Organic C stock | gaussian | permaculture age | 4.36 | 52 | 0.037 | location, texture class |
| Total N | nbinom2 | management | 662.2 | 2147 | <0.001 | location, texture class |
| P | nbinom2 | management | 3.15 | 78 | 0.076 | location, texture class, pH |
| K | nbinom2 | management | 21.15 | 78 | <0.001 | location, texture class, pH |
| Mg | genpois | management | 24.58 | 78 | <0.001 | location, texture class, pH |
| B | tweedie | management | 8.60 | 77 | 0.003 | location, texture class, pH |
| Cu | gaussian | management | 0.10 | 78 | 0.750 | location, texture class, pH |
| Mn | gaussian | management | 0.70 | 78 | 0.404 | location, texture class, pH |
| Zn | genpois | management | 31.48 | 78 | <0.001 | location, texture class, pH |
| Total PLFA | nbinom2 | management | 7.31 | 78 | 0.007 | location, texture class, pH |
| Bacteria PLFA | genpois | management | 9.92 | 78 | 0.002 | location, texture class, pH |
| Fungi PLFA | nbinom2 | management | 3.89 | 78 | 0.049 | location, texture class, pH |
| Fungi/bacteria PLFA ratio | gaussian | management | 0.86 | 78 | 0.353 | location, texture class, pH |
| Gram−/gram+ PLFA ratio | gaussian | management | 2.77 | 78 | 0.096 | location, texture class, pH |
| Mykorrhizae/fungi PLFA ratio | gaussian | management | 0.62 | 71 | 0.430 | location, texture class, pH |

Structure of generalized linear mixed models fitted in R using the glmmTMB package. χ^2 values and *p* values were obtained by Type II Wald χ^2 tests on model outcomes. Significant *p* values are highlighted in bold, and statistical trends are in italics.

solution (CAT) and measured with ICP-OES (A 6.4.1). Values below the detection threshold were taken as zero. For soil variables, a weighted mean was calculated for samples from the two sampling horizons to obtain a value for the first 30 cm of topsoil. For soil type comparison, samples were classified manually “by feel” by well-trained and experienced laboratory staff into seven soil texture classes with decreasing particle size (D 2.1)¹⁰⁶.

Soil organic carbon stocks were calculated as soil organic carbon concentration multiplied by bulk density and horizon depth (30 cm). Values for soil phosphate and potassium oxide concentrations were converted to phosphorus and potassium concentrations using respective molar masses.

Abundance and structure of soil microbial communities

To investigate the microbial community, PLFA was analyzed in soil samples. The extraction procedure followed the method by Bligh and Dyer¹⁰⁷ and White et al.¹⁰⁸ with small modifications by Kenngott et al.¹⁰⁹. Phospholipids were extracted from 2 g of freeze-dried soil using a mixture of 2 mL chloroform, 4 mL methanol, and 1.6 mL phosphate buffer as extraction solution. Extracts were agitated for 1 h in an overhead shaker (16 rpm). Then, phospholipids were separated from the neutral lipids and glycolipids using solid-phase extraction cleanup (Chromabond, Macherey-Nagel, Düren, Germany). Eluted PLFAs were transesterified with a 0.25 molar solution of methanolic trimethylsulfonium hydroxide¹¹⁰. The extracts were analyzed via GC-FID (Varian CP-3800, Varian, Darmstadt, Germany). Quantification was based on external calibration with reference standards. The PLFA used as quantitative standards and as biomarkers for soil microbial community groups were: i15:0 and i17:0 for gram-positive

bacteria, 16:1 ω 7c and 18:1 ω 9c for gram-negative bacteria^{111,112}, 16:1 ω 5c for arbuscular mycorrhizal fungi^{113,114}, 18:2 ω 6c for saprophytic fungi^{112,115,116} and 20:4 ω 6c for protozoa^{117,118}. To compensate for differences in mass weight of individual biomarkers, molar concentrations per gram of soil dry matter were used. Total PLFA corresponds to the sum of individual PLFA biomarkers and is used as proxy for the total viable microbial biomass¹¹⁹. For evaluation of specific groups (bacteria, fungi, etc.) corresponding biomarkers were summed up as well. Changes in the chemotaxonomic structure of microbial communities were evaluated using the fungi-to-bacteria, the arbuscular mycorrhizal-to-saprophytic fungi, and the gram-positive to-gram-negative bacteria ratios.

Additional data

The data of Lüscher et al.³⁵ was used for additional comparison of biodiversity variables. Here, the dataset is published as supplementary information to the respective article (<https://doi.org/10.1890/15-1985.1>)³⁵. From this dataset, all European regions with either arable crops, grassland, horticulture, or mixed culture were selected. Special land use types like olives or vineyards were omitted. For comparability with this study only areal plots were used for evaluation. As in this study, only fully determined earthworm species were counted for species richness comparison. For each farm, including permaculture sites from this study, the share of the area with tree cover was calculated. For statistical analysis, the farm ID of this additional biodiversity dataset was treated as a location variable from this study and management (conventional or organic) as a management variable from this study (permaculture, control).

Table 4 | Results of post hoc comparisons

| Response variable | Pairwise comparison | | z/t value | p value |
|----------------------------|---------------------|--------------|-----------|------------------|
| Earthworm abundance | permaculture | control | 5.46 | <0.001 |
| | permaculture | conventional | 3.69 | 0.001 |
| | permaculture | organic | 2.78 | 0.028 |
| | control | conventional | 0.84 | 0.833 |
| | control | organic | 0.03 | 1.000 |
| | conventional | organic | 1.78 | 0.285 |
| Earthworm species richness | permaculture | control | 2.43 | 0.073 |
| | permaculture | conventional | 0.98 | 0.762 |
| | permaculture | organic | 0.16 | 0.999 |
| | control | conventional | 1.04 | 0.728 |
| | control | organic | 1.77 | 0.291 |
| Plant species richness | permaculture | control | 6.66 | <0.001 |
| | permaculture | conventional | 3.96 | <0.001 |
| | permaculture | organic | 3.65 | 0.002 |
| | control | conventional | 3.60 | 0.002 |
| | control | organic | 3.76 | 0.001 |
| Tree area | conventional | organic | 0.64 | 0.920 |
| | permaculture | conventional | 2.87 | 0.011 |
| | permaculture | organic | 2.89 | 0.011 |
| Bulk density | conventional | organic | 0.14 | 0.990 |
| | permaculture | control | 10.04 | <0.001 |
| | permaculture | arable | 10.04 | <0.001 |
| | permaculture | grassland | 7.63 | <0.001 |
| | control | arabe | 2.08 | 0.159 |
| | control | grassland | 0.03 | 1.000 |
| Organic C content | arable | grassland | 9.64 | <0.001 |
| | permaculture | control | 7.19 | <0.001 |
| | permaculture | arable | 7.97 | <0.001 |
| | permaculture | grassland | 2.41 | 0.076 |
| | control | arabe | 1.00 | 0.750 |
| | control | grassland | 3.84 | <0.001 |
| Organic C stock | arable | grassland | 20.78 | <0.001 |
| | permaculture | control | 4.60 | <0.001 |
| | permaculture | arable | 3.26 | 0.006 |
| | permaculture | grassland | 0.40 | 0.978 |
| | control | arabe | 0.85 | 0.832 |
| | control | grassland | 2.64 | 0.041 |
| Total N | arable | grassland | 18.19 | <0.001 |
| | permaculture | control | 8.34 | <0.001 |
| | permaculture | arable | 9.30 | <0.001 |
| | permaculture | grassland | 4.11 | <0.001 |
| | control | arabe | 3.82 | <0.001 |
| | control | grassland | 1.00 | 0.751 |
| | arable | grassland | 23.38 | <0.001 |

Z/t values are given as absolute numbers. Significant *p* values are presented in bold font, while *p* values indicating a statistical trend are presented in italic font.

The data of Poeplau et al.³⁶ was used for additional comparison of soil variables. Here the dataset is published in the OpenAgrar repository (<https://doi.org/10.3220/DATA20200203151139>)¹²⁰. From this dataset, all sites were

selected that were sampled at depths of 0–10 cm and 10–30 cm, contained minerals soils (organic soils omitted), were sampled on cropland or on grassland (special permanent crops omitted) and values available for soil organic carbon, total nitrogen, and bulk density. Soil texture classes of this dataset were converted to the seven soil texture classes used in this study¹⁰⁵. For statistical analysis, the point ID of this additional soil dataset was treated as a location variable from this study, and land use type (cropland or grassland) as a management variable from this study (permaculture, control).

Statistics

Statistical analysis was carried out using R (R 4.2.1, R Development Core Team 2022). For each response variable (Table 3) a generalized linear mixed model using the ‘glmmTMB’ package was fitted with management as fixed predictor variable¹²¹. The management variable comprises factor levels of permaculture and control field as well as organic and conventional agriculture or arable land and grassland in case of added literature datasets (see above). To account for the paired sampling design of permaculture sites and corresponding control fields, location was included as a random factor for each response variable. For soil-related response variables, soil texture class and pH value were included as random factors to account for possible differences in soil type. For organic carbon and total nitrogen levels, pH value was not included as these parameters do not depend on soil pH¹²².

For organic carbon stocks, a second model was fitted with age as predictor variable and location and soil texture class as random factors to estimate carbon sequestration. To set today as a baseline, the age of the permaculture sites was set to zero, and the age of the paired control fields was set to the negative age of the corresponding permaculture site. This calculation was done only for six permaculture sites, where previous land use equalled land use of control fields. Further, this calculation is based on the assumption that the carbon level was originally sufficiently equal on-site pairs and did not change on control fields.

Response variables with percentage values that are limited to values between 0 and 1 were fitted, assuming a beta distribution (beta or ordbeta families). All other response variables were fitted subsequently assuming a normal (gaussian family), Poisson (companies or generous families), or negative binomial (nbinom1 or nbinom2 families) distribution, depending on model diagnostics. Residuals and diagnostics of models were checked using the ‘DHARMa’ package to control for model misspecification problems such as multicollinearity, over/underdispersion, zero-inflation residual, spatial, and temporal autocorrelation¹²³. If more than one distribution family produced a model with acceptable diagnostics, we selected the model according to the Akaike Information Criterion¹²⁴. If none of these families produced a model with acceptable diagnostics, we fitted another model assuming a Tweedie (Tweedie family) distribution and checked model diagnostics.

The significance of the predictor variable was evaluated with a Type II Wald χ^2 test using the Anova function of the ‘car’ package (Table 3)¹²⁵. Post hoc pairwise comparisons of management factor levels were done with Tukey correction using the ‘emmeans’ package (Table 4)¹²⁶. The ggpredict function of the ‘ggeffects’ package was used to compute model-predicted means and 95% confidence intervals¹²⁷.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The data that supports the findings of this study is available in The Knowledge Network for Biocomplexity (KNB) with the identifier <https://doi.org/10.5063/F1J964VN>¹²⁸.

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Author contributions

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Correspondence and requests for materials should be addressed to Julius Reiff.

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