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From Mor to Mull: Humus forms reflect forest floor temporal dynamics and ecosystem change in northwest Germany

Vom Rohhumus zum Mull: Humusformen als Indikator für die zeitliche Dynamik in Waldökosystemen in Nordwestdeutschland

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Abstract

Humus form classification provides a powerful diagnostic tool for assessing forest soil conditions and tracking ecosystem change. As integrative indicators, humus forms reflect long-term interactions among climate, deposition, vegetation, and management, offering insights into nutrient cycling, microbial activity, and organic matter turnover. In this study, we analyzed humus form dynamics over a span of more than three decades (1990–2023) from the three German National Forest Soil Inventories (NFSI; Bodenzustandserhebung (BZE)), which are conducted approximately every 16 years. The NFSI samples forest monitoring plots systematically on an 8 × 8 km raster grid; for northwest Germany (Schleswig-Holstein, Lower Saxony, Saxony-Anhalt, Hesse, Bremen, and Hamburg), this corresponds to a regional subset of 465 plots in the most recent inventory. For temporal comparisons, the analysis focused on a subset of 319 plots, consistently surveyed across all three inventories and based on harmonized humus form definitions from the most recent version of the German humus form reference base. Our analysis shows a clear shift toward humus types with generally faster organic matter turnover: Mull increased from 23% of sites in 1990 to 31% in 2023, while Mor declined from 20% to 9% over the same period. These shifts were most pronounced on nutrient-poor substrates such as sandy soils and Buntsandstein, whereas nutrient-rich substrates (e.g., limestone, basalt, marl) remained comparatively stable. Correspondingly, forest floor thickness also varied through time, decreasing significantly from the first to the second inventory and then increasing significantly again by the third, largely reflecting greater accumulation in the litter (Ol) and fermented (Of) layers, while the humified (Oh) layer remained relatively stable.

Potential drivers of humus form changes include persistently high nitrogen inputs, reduced sulfur deposition, forest liming, conversion toward broadleaf stands, rising temperatures, and episodic summertime droughts, as well as changes in forest stand structure and regeneration. While the shift toward Mull and Moder may enhance nutrient availability and forest productivity, it may also affect long-term carbon storage in the forest floor, potentially increasing nitrate leaching risks and altering greenhouse gas fluxes. Overall, our findings demonstrate that humus forms are a sensitive indicator of environmental changes and capture the cumulative impacts of deposition, management, climate, and substrate on forest ecosystem functioning.

Keywords

National Forest Soil Inventory (NFSI), long-term soil monitoring, organic matter turnover, nitrogen deposition, climate change, forest liming

Zusammenfassung

Die Klassifikation von Humusformen ermöglicht eine integrierte Bewertung von Waldbodenprozessen und ihrer langfristigen Entwicklung. Auf Basis von drei Erhebungen der Bodenzustandserhebung im Wald (BZE I 1990, BZE II 2006, BZE III 2023) wurde die Veränderung von Humusformen in Nordwestdeutschland untersucht. Die Analyse basiert auf 319 Waldflächen, die in allen drei Inventuren wiederholt erfasst und anhand harmonisierter Humusform-Definitionen ausgewertet wurden.

Die Ergebnisse zeigen eine deutliche Verschiebung der Humusformen von der BZE I zur BZE III von Rohhumus zu Moder und Mull. Während der Anteil von Mull von 23 % auf 31 % anstieg, ging Rohhumus von 20 % auf 9 % zurück. Die stärksten Veränderungen traten auf nährstoffarmen Substraten auf, z. B. wie unverlehmter Sand, während auf nährstoffreichen Standorten, z. B. Basalt, die Humusformen vergleichsweise stabil blieben. Parallel dazu veränderte sich die Mächtigkeit der Auflage deutlich, mit einer Abnahme zwischen der ersten und zweiten sowie einer erneuten Zunahme bis zur dritten Inventur, vor allem bedingt durch Veränderungen der Streu- und Fermentationsschichten (L- und F-Lage), während die Feinhumusschicht (H-Lage) weitgehend stabil blieb. Die beobachteten Trends deuten auf veränderte Umsatzprozesse organischer Substanz hin, die durch das Zusammenwirken von abnehmender Schwefeldeposition, anhaltend hohen Stickstoffeinträgen, Waldkalkung, Veränderungen der Baumartenzusammensetzung sowie klimatischen Faktoren wie Erwärmung und episodischer Sommertrockenheit beeinflusst werden. Insgesamt unterstreichen die Ergebnisse die Eignung von Humusformen als empfindliche Indikatoren für langfristige Umweltveränderungen in Waldökosystemen.

Schlüsselwörter

Bodenzustandserhebung im Wald (BZE), Bodenmonitoring, Umsatz organischer Substanz, Stickstoffdeposition, Sommertrockenheit, Waldkalkung

1 Introduction

Over recent decades, European forest ecosystems have been strongly shaped by numerous external drivers that have altered different soil processes, nutrient cycles, vegetation dynamics, and ecosystem functioning. Atmospheric deposition of sulfur and nitrogen, climate change, droughts, insect outbreaks, and forest management have all modified processes both above- and belowground. These changes have affected not only tree species composition and biodiversity (Bundesministerium für Landwirtschaft, Ernährung und Heimat 2024), but also soil microbial activity, organic matter turnover, nutrient availability, and soil structure (Paar et al. 2016, Evers et al. 2019, 2022, Du et al. 2025).

Soils play a central role in mediating the impacts these external drivers have on ecosystem function and health. The condition of forest soils, particularly the forest floor layer, reflects the integrated effect of environmental changes. In northwestern Germany, as in much of Central Europe, long-term inputs of sulphur (S) and nitrogen (N) have had strong effects on forest soil chemistry and biology (De Vries et al. 2006). Elevated S deposition during the mid-20th century accelerated acidification, depleted base cations such as calcium, magnesium, and potassium, and reduced microbial activity and organic matter decomposition (Ulrich 1999, Meesenburg et al. 2019). Although stricter air pollution control policies have substantially reduced S inputs, the legacy effects of historical acidification remain evident in many soils (Ahrends, Fortmann & Meesenburg 2022, Zethof et al. 2024). In contrast, N deposition has remained at high levels in recent decades, particularly in northwestern Germany (Schaap et al. 2018), further contributing to acidification, altering nutrient balances, and driving changes in ecosystem biodiversity (Flechard et al. 2020, Du et al. 2025).

In addition to atmospheric deposition, other stressors such as climate change, disturbances, and forest management also affect forest soils. Specifically, rising temperatures accelerate decomposition processes, whereas recurrent droughts can constrain microbial activity and slow organic matter breakdown, often leading to the accumulation of undecomposed organic matter in the forest floor (Qu et al. 2023). Insect outbreaks have been shown to alter litter input and microclimatic conditions, which can cause short-term nutrient release and changes in microbial communities (Leal et al. 2023, Shang, Zuo & Liu 2024). In addition, forest management practices, through activities such as thinning, harvesting, and tree species selection, can influence litter input and its chemical and physical characteristics, which in turn affect nutrient cycling, soil structure, and water infiltration. Finally, forest liming, which has been widely applied in parts of Germany, directly modifies soil chemistry by increasing pH, enhancing base cation availability, which in turn stimulates organic matter decomposition thereby improving nutrient supply (Evers et al. 2019, Van Straaten et al. 2023).

Humus form classification provides a structured way to integrate information on litter inputs, decomposition processes, and nutrient cycling into recognizable morphological types (Ponge 2003, Zanella et al. 2011, Wachendorf et al. 2023). Because humus forms reflect both natural and anthropogenic influences, they are particularly useful for monitoring long-term soil changes and for assessing forest soil condition in a changing environment. In this study, we used the German National Forest Soil Inventory (NFSI; Bodenzustandserhebung in German) to assess regional- and long-term changes in humus forms. The NFSI provides repeated, large-scale data on forest soils collected every 15 to 16 years (Wellbrock et al. 2019). Using the three NFSI surveys (1990, 2006, and 2023), we investigated changes in humus forms in northwestern Germany and examined how these relate to soil chemical properties. Our primary objective was to assess temporal and spatial dynamics in humus form development and to explore the potential drivers of observed changes. A secondary objective was to evaluate how different humus types correspond to soil chemistry, including C:N ratios and carbon stocks. We hypothesize that humus forms have shifted toward more biologically active types as a result of long-term environmental change, driven by warming and reduced acidification but moderated by episodic drought.

2 Materials and Methods

2.1 *Humus form classification and sampling*

Within the framework of the German National Forest Soil Inventory (NFSI), humus forms were classified at each monitoring site during three inventories, specifically in 1990, 2006, and 2023. The NFSI systematically sampled forested sites across Germany using a predefined 8 × 8 km grid. This study examines the development and trajectories of humus forms across four federal states in northwest Germany: Lower Saxony, Hesse, Saxony-Anhalt, Schleswig-Holstein, and the two city-states of Bremen and Hamburg. The number of plots varied across the three inventories, with 447 plots sampled in the first, 414 in the second, and 465 in the most recent inventory. For the change analysis, we restricted the dataset to the 343 plots sampled consistently across all three inventories. Differences in plot numbers and overlap between inventories were due to shifts in the sampling grid (between NFSI I and II in Lower Saxony), land-use changes, and the identification of new forested plots over time. From this subset, we excluded organic sites (n = 5), as their ecological processes differ from those on mineral soils. We also excluded sites where classification system differences (n = 19) between the inventories prevented us from identifying comparable categories in earlier inventories. The final dataset therefore comprised 319 plots.

Humus forms were assigned based on the classification system available at the time of each inventory. In the first NFSI, humus forms were classified according to the methodology described in the NFSI manual (Bundesministerium für Ernährung 1990). The second inventory followed the fifth edition of the German Soil Survey Guidelines (KA5; Ad-hoc-Arbeitsgruppe Boden, 2005), and the third inventory used the sixth edition of these guidelines (KA6; Ad-hoc-Arbeitsgruppe Boden, 2024). The methodology applied in the most recent inventory is described in detail by Wachendorf et al. (2023).

Although the humus form classification system was refined over three decades, the basic principles remained consistent. Classification is based on the composition, morphology, structure, and decomposition stage of accumulated organic matter. In Germany, the system adopts a morphogenetic approach, using diagnostic horizons and properties to infer the processes and pathways involved in humus formation. Each classification system employed a hierarchical structure, organizing humus forms into distinct levels. At the broadest level, hydrological conditions were distinguished, such as anaerobic versus aerobic environments. These categories were further subdivided based on morphological characteristics, including the presence or absence of a highly humified Oh layer. Both the KA5 and KA6 classification systems have a clearly defined hierarchy, progressing from Division to Class to Type, Sub-type, and finally Variety (Ad-hoc-Arbeitsgruppe Boden 2005, 2024).

Similar to the European Humus Forms Reference Base (Zanella et al. 2011), the German system recognizes a sequence of aeromorphic and aero-hydromorphic humus forms, ranging from Mull to forms with an Oh horizon (Moder to Mor). The revised KA6 classification system further introduces two additional categories: Initial and Degraded humus forms, the latter which may arise from either anthropogenic or natural processes (Wachendorf et al. 2023). To ensure comparability across inventories, we developed a translation table (Table S1) that aligns the most closely corresponding humus forms between the three classification systems. A notable update in the most recent version was the redefinition of "Mor-like Moder" as "Moder-like Mor," thereby reassigning these sites to the Mor category. For consistency, all results are reported using the KA6 nomenclature, with earlier inventories translated accordingly. It should be acknowledged that, despite formal training and the use of classification keys, some subjectivity remains in humus form identification, particularly at finer hierarchical levels (sub-type and variety). To minimize variability, classifications were aggregated at the Type level, with L-Mull and F-Mull combined into Mull, as this distinction was not present in the first NFSI. All data analyses presented here were conducted at this level.

During each inventory, humus forms were classified at eight satellite sampling points located 10 m from the central soil pit (Wellbrock et al. 2022). At these same points, the thickness of each forest floor layer (L, Of, and Oh) was measured to compliment humus form classification and assess changes in organic matter accumulation and decomposition dynamics.

2.2 *Statistical analysis*

Changes in humus form types (Mull, Moder, Mor) over time across the three forest inventories were visualized using Sankey plots, both overall and stratified by substrate type. Differences in forest floor layer thickness between inventories were analyzed using linear mixed-effects models to account for repeated measurements on the same plots across inventories, with plot identity included as a random effect and inventory treated as a fixed effect. Model assumptions were evaluated using graphical and numerical residual diagnostics. Forest floor layer thicknesses were log-transformed where necessary to improve residual normality and variance homogeneity. Pairwise differences between inventories were assessed using Tukey-adjusted post hoc comparisons based on estimated marginal means.

Relationships between humus forms, their transitions between inventories, and soil chemical properties (carbon stocks, C:N ratios, pH, and base saturation) in the forest floor and mineral topsoil were evaluated using Kruskal–Wallis tests followed by Dunn's post-hoc tests with Holm correction. Statistical analyses were conducted in R version 4.2.2 (R Core Team 2022).

3 Results

In the most recent survey (NFSI III, 2023), Mull humus forms were recorded at 27% of the 465 sampling points, Moder at 55%, Mor at 8%, and Initial humus forms at 10%. Degradation humus forms were observed only once (Tab. S2). The three dominant humus forms (Mull, Moder, and Mor) were distributed across the study region (Fig. 1), with broad geographic patterns evident. Mull was most common in the

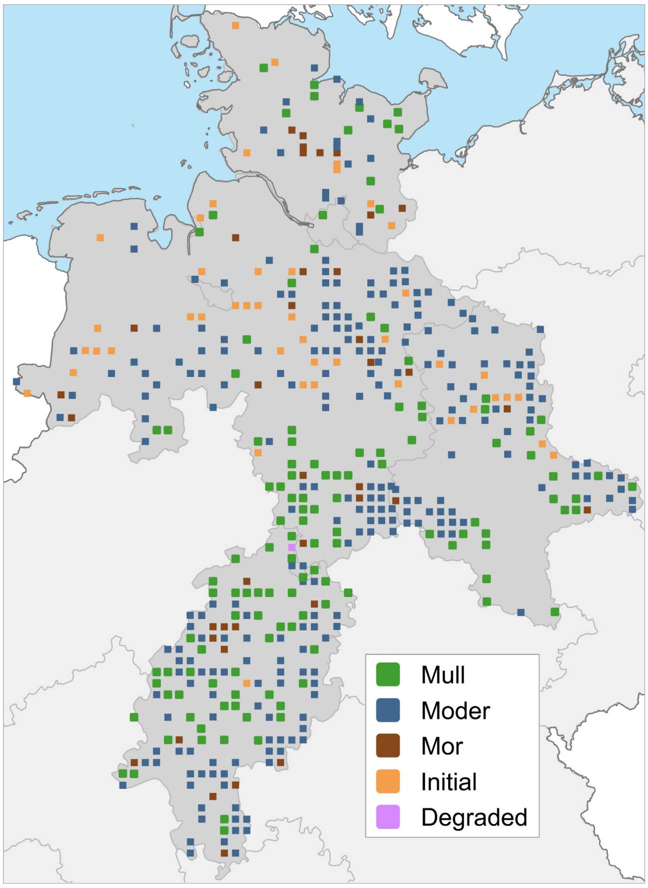

Fig. 1: Spatial distribution of humus form types in northwest Germany observed during the third NFSI in 2023.

Abb. 1: *Räumliche Verbreitung der Humusformtypen in Nordwestdeutschland, erfasst in der dritten Bodenzustandserhebung im Wald (BZE III) im Jahr 2023.*

southern parts of Lower Saxony, scattered throughout Hesse, and in eastern Saxony-Anhalt. Moder was widespread, with particularly high proportions in the Harz Mountains and the Lüneburger Heathlands. Mor occurred across northwestern Germany without clear clustering. Initial humus forms were more frequent in the sandy lowland area, with only a few occurrences in upland regions.

Humus forms differed markedly in their associated soil properties. Based on data from the second forest soil inventory, forest-floor carbon stocks increased significantly from Mull to Moder to Mor (Fig. 2a), whereas mineral soil (0–5 cm) carbon stocks did not differ significantly among humus forms (Fig. 2b). In contrast, forest-floor C:N ratios showed no significant variation among humus types (Fig. 2c), while mineral soil C:N ratios increased significantly from Mull to Moder to Mor (Fig. 2d). Both forest floor and mineral soil pH also varied significantly among humus forms, with Mull exhibiting the highest pH, followed by Moder, and Mor showing the lowest (Fig. 2e, f).

Soil substrate and forest composition further influenced the distribution of humus forms. In NFSI III, substrates typically associated with lower base saturation (e.g., Buntsandstein, sandy soils, shale, quartzite) were predominantly associated with Moder (67%), whereas comparatively richer parent materials (e.g., limestone, basalt, diabase, Zechstein, marl) most frequently supported Mull (61%; Tab. S3). Similarly, in NFSI II (2006), forest composition showed clear associations: deciduous-dominated stands were primarily linked to Mull (60% of deciduous sites; Table S4), while coniferous stands were mostly characterized by Moder (86%), with spruce forests exhibiting particularly high proportions of Mor (38%).

Temporal comparisons across the three inventories showed clear shifts in humus form types. Mor declined from 20% in NFSI I to 18% in NFSI II and further to 9% in NFSI III, while Mull increased from 23% to 33% and then stabilized at 31% in the most recent inventory. Moder remained the dominant humus form throughout all inventories (56%, 49%, and 60%, respectively), with most transitions occurring from Mor to Moder and from Moder to Mull (Fig. 3). Spatially, although most changes were scattered without strong regional

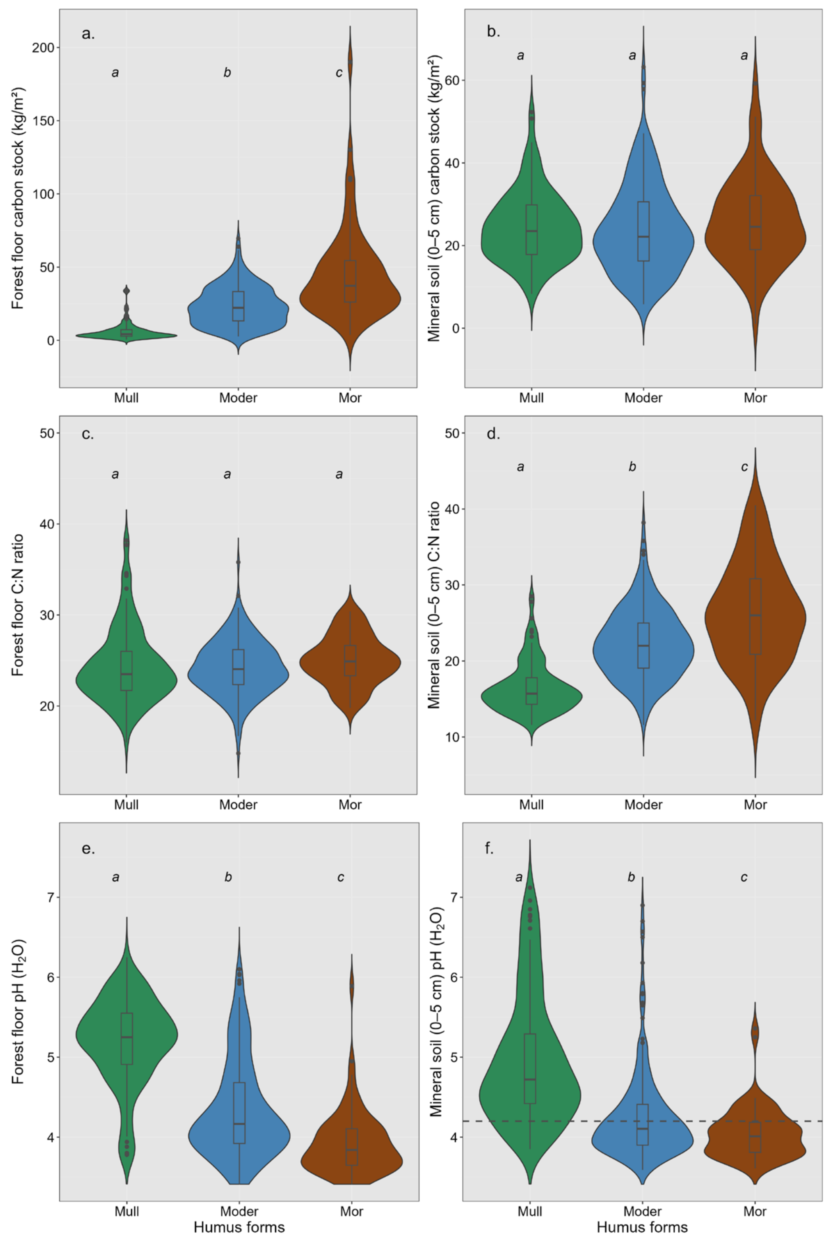

Fig. 2: Carbon stocks, C:N ratios, and pH across the three humus forms (Mull, Moder, Mor) in the forest floor and upper mineral soil. Panels (a, c, e) show forest floor properties (carbon stock, C:N ratio, pH), and panels (b, d, f) show corresponding properties of the 0–5 cm mineral soil layer. Violin plots display data distributions; boxplots indicate medians and interquartile ranges. Letters denote statistically significant differences among humus forms ($p < 0.05$). In panel (f), the dashed horizontal line at pH 4.2 marks the transition between the aluminum buffer range below and the base cation buffer range above.

Abb. 2: *Kohlenstoffvorräte, C:N-Verhältnisse und pH-Werte in den drei Humusformentypen (Mull, Moder, Rohhumus) in der Auflage und im obersten Mineralboden. Die Panels (a, c, e) zeigen Eigenschaften der Auflage (C-Vorrat, C:N-Verhältnis, pH), die Panels (b, d, f) die entsprechenden Eigenschaften der Mineralbodenstufe 0–5 cm. Violin-Plots zeigen die Datenverteilung; Boxplots Median und Interquartilsabstand. Buchstaben kennzeichnen signifikante Unterschiede zwischen Humusformen ($p < 0.05$). In Panel (f) markiert die gestrichelte horizontale Linie bei pH 4,2 den Übergang zwischen Aluminium-Pufferbereich (darunter) und Basenkationen-Pufferbereich (darüber).*

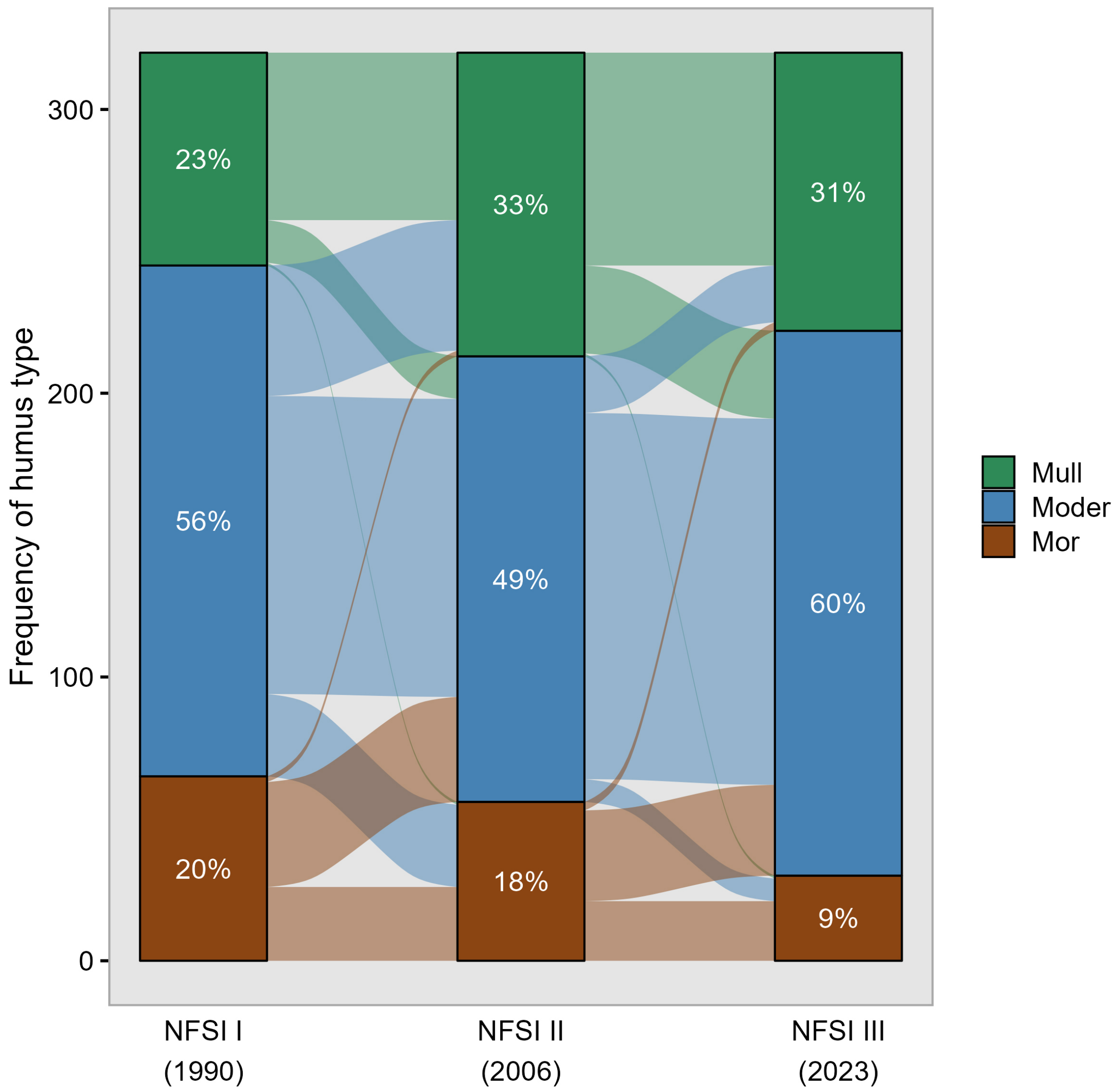

Fig. 3: Temporal changes in humus form types across three National Forest Soil Inventories (NFSI; 1990, 2006, 2023). The vertical bars show the frequency of points different humus form types for each inventory, while the connecting flow bars illustrate transitions of humus forms between categories over time. This analysis only included sampling points where humus forms types were classified in all three inventories. It excluded organic sites and those categorized as either initial or degraded in the latest inventory, where these types were newly introduced.

Abb. 3: *Zeitliche Veränderungen der Humusformtypen in drei Inventuren der Bodenzustandserhebung im Wald (BZE 1990, 2006, 2023). Die vertikalen Balken zeigen die Häufigkeit der Humusformtypen je Inventur; die verbindenden Flussbänder veranschaulichen Übergänge zwischen Typen über die Zeit. Berücksichtigt wurden nur Probepunkte, an denen Humusformen in allen drei Inventuren bestimmt wurden. Organische Standorte sowie Standorte, die in der letzten Inventur als Initial- oder Degradationshumusformen klassifiziert wurden, wurden ausgeschlossen.*

clustering, the Harz Mountains and the Lüneburger Heathlands showed more frequent transitions from Mor to Moder (Fig. S1). Changes in humus forms also varied with soil parent material: nutrient-poor substrates such as sandy soils, Buntsandstein, and shale exhibited more pronounced transitions (Fig. 4 a–d), whereas nutrient-rich substrates including basalt or diabase, limestone, loess, clay, and marl remained comparatively stable (Fig. 4 e–h).

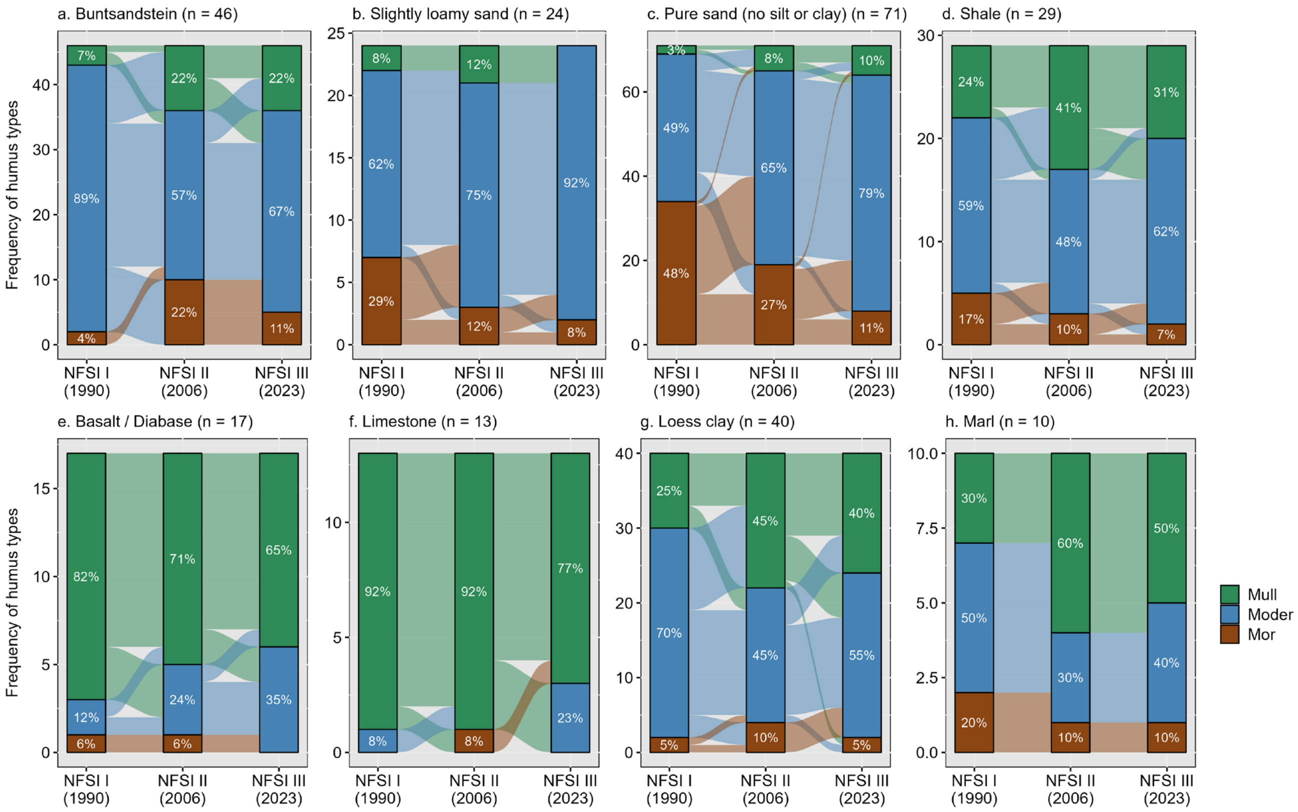

Fig. 4: Development of humus form types across three National Forest Soil Inventories (NFSI I–III), shown as Sankey diagrams stratified by substrate groups. The upper panel represents nutrient-poor substrates and the lower panel nutrient-rich substrates. Flow widths indicate the number of plots transitioning between humus forms, and percentages show relative frequencies within each substrate group. Intermediate substrate types with low replication are not shown.

Abb. 4: *Entwicklung der Humusformtypen über drei Inventuren der Bodenzustandserhebung im Wald (BZE I–III), dargestellt als Sankey-Diagramme nach Substratgruppen. Das obere Panel zeigt nährstoffarme, das untere Panel nährstoffreiche Substrate. Die Breite der Flüsse entspricht der Anzahl der Flächen mit Übergängen zwischen Humusformentypen; Prozentwerte geben die relativen Häufigkeiten innerhalb der jeweiligen Substratgruppe an. Substrattypen mit geringer Replikation sind nicht dargestellt.*

Across the same period, the forest floor exhibited marked temporal variation in layer thickness (Fig. 5), decreasing from the first to the second inventory and increasing again in the third. This overall pattern was primarily driven by a significant reduction in the litter (L) layer between the first and second inventories, followed by a pronounced and significant increase in the fermented (Of) layer between the second and third. Forest-floor thickness also varied among soil substrate groups, with thick forest floor layers found on nutrient-poor substrates compared to richer ones, whereby the overall temporal trends observed were similar across all substrate types analyzed (Fig. S2).

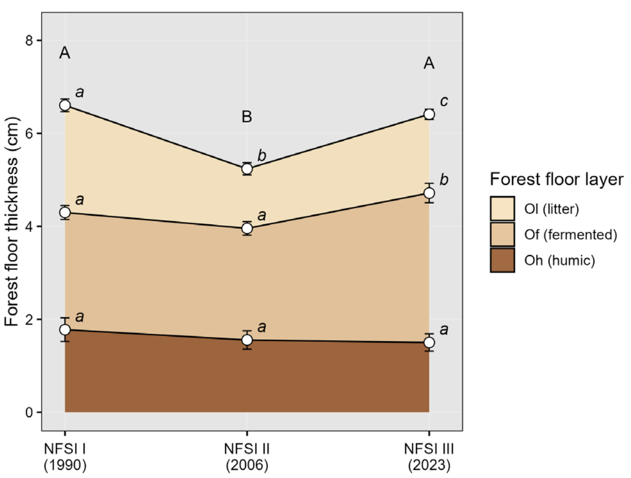

Fig. 5: Stacked area plot showing mean thickness (cm) of forest floor layers (Ol – litter, Of – fermented, Oh – humic) across all three NFSI inventories (n = 319). Error bars represent 95% confidence intervals. Lowercase letters indicate statistically significant differences between inventories for individual layers, and uppercase letters indicate differences in total forest-floor thickness, based on linear mixed-effects models with inventory as a fixed effect and plot as a random effect (α = 0.05).

Abb. 5: *Gestapeltes Flächendiagramm zur zeitlichen Veränderung der mittleren Auflagemächtigkeit (cm) und ihrer Horizonte (Ol, Of, Oh) in drei Inventuren der Bodenzustandserhebung im Wald (n = 319). Fehlerbalken zeigen 95%-Konfidenzintervalle. Signifikante Unterschiede zwischen Inventuren basieren auf linearen gemischten Modellen unter Berücksichtigung wiederholter Messungen (α = 0.05).*

Humus form changes between inventories (NFSI II and NFSI III) were closely linked to underlying mineral soil chemistry, as reflected in Fig. 6, which shows humus form transitions in relation to topsoil pH and base saturation (0–30 cm). Sites where Moder in NFSI II changed to either Mull or Mor in NFSI III showed no significant differences in soil chemistry compared with sites where the humus form remained unchanged. In contrast, sites that transitioned to Moder (whether from Mull or Mor), exhibited significant differences in both soil pH and base saturation relative to sites where Moder remained stable.

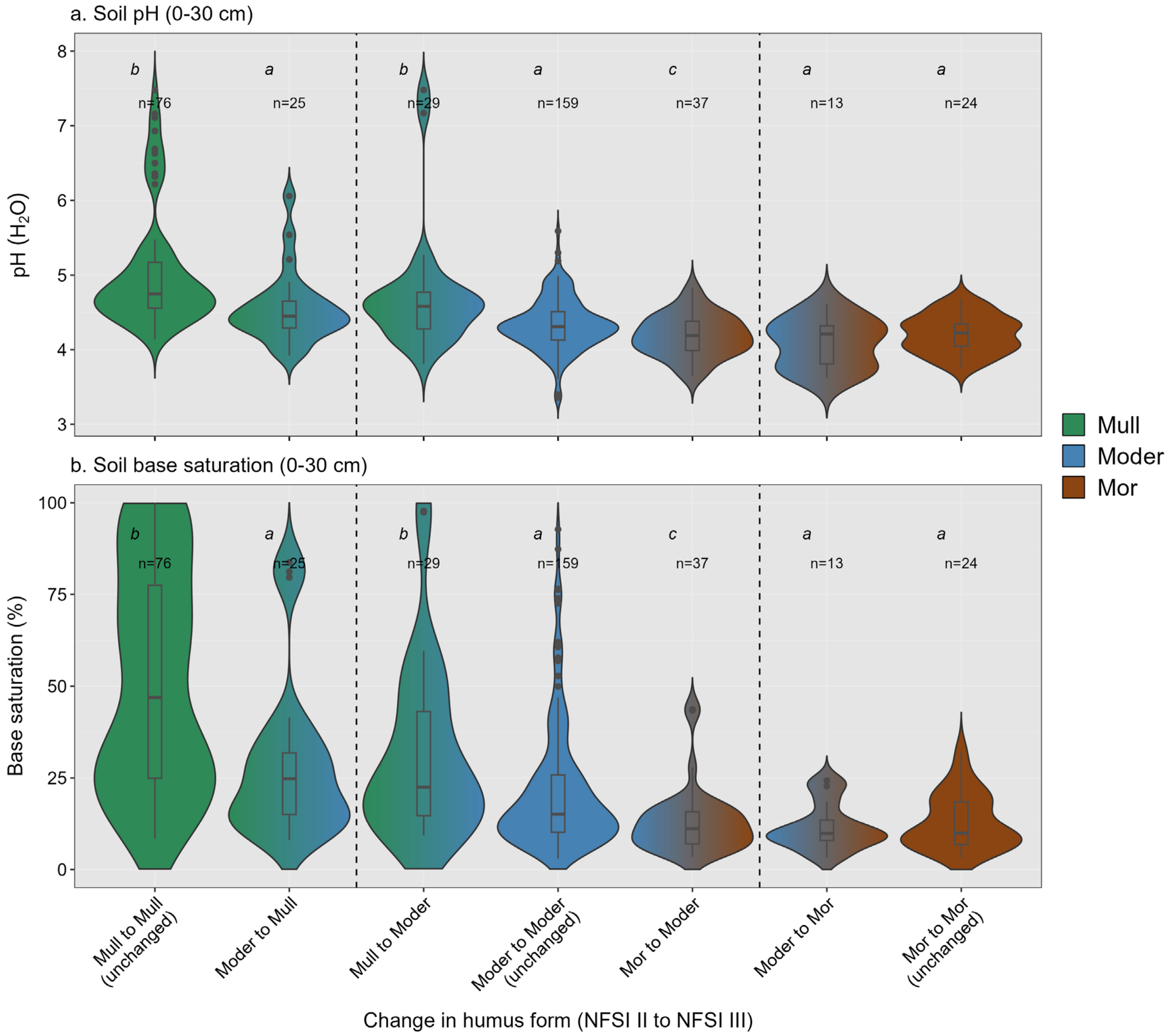

Fig. 6: a) Soil pH (H_2O, 0–30 cm); b) and base saturation (0–30 cm) across humus form transitions (NFSI II → NFSI III). Changes in humus form reflect the mineral soil chemistry at each site from the NFSI II (2006) dataset. The x-axis shows the direction of humus form change, including unchanged sites; vertical dashed lines separate groups by the humus form recorded in NFSI III. Colors denote humus form types (Mull, Moder, Mor), with gradient fills indicating humus form transitions. Violin plots show data distribution; boxplots indicate median and interquartile range. Letters indicate significant differences within each group defined by the humus form in the last inventory (NFSI III) using Dunn test with Holm adjustment ($p < 0.05$), and n values show sample sizes. Transitions with fewer than five observations (specifically, Mull to Mor (n = 1) or Mor to Mull (n = 4)) were excluded due to the small sample size.

Abb. 6: *a) Boden-pH (H_2O) 0–30 cm Mineralboden und b) Basensättigung (0–30 cm) in Abhängigkeit von Humusformtyp-Übergängen (BZE II → BZE III). Die Änderungen der Humusformtypen werden in Bezug zur Mineralbodenchemie der jeweiligen Standorte aus dem Datensatz der BZE II (2006) gesetzt. Die x-Achse zeigt die Richtung der Humusformtypänderung einschließlich unveränderter Standorte; vertikale gestrichelte Linien trennen Gruppen nach der in BZE III erfassten Humusform. Farben kennzeichnen Humusformtypen (Mull, Moder, Rohhumus), Farbverläufe die Übergänge. Violin-Plots zeigen die Datenverteilung; Boxplots Median und Interquartilsabstand. Buchstaben kennzeichnen signifikante Unterschiede innerhalb jeder durch die Humusform der letzten Inventur (BZE III) definierten Gruppe (Dunn-Test mit Holm-Korrektur, p < 0.05); n-Werte geben Stichprobengrößen an. Übergänge mit weniger als fünf Beobachtungen (Mull → Rohhumus (n = 1) bzw. Rohhumus → Mull (n = 4)) wurden aufgrund der geringen Stichprobengröße ausgeschlossen.*

4 Discussion

4.1 *Humus forms as indicators of site and soil chemistry*

Our results confirm that humus forms are reliable indicators of site conditions and soil biochemical status, reflecting their strong associations with multiple soil parameters such as forest-floor carbon stocks, mineral soil C:N ratios, pH, and base saturation (Fig. 2 and Fig. 6). These relationships show how humus forms integrate biological activity with the chemical and physical conditions of the soil. Data from the second NFSI in 2006 show that carbon stocks in the forest floor layer varied significantly with humus type, being highest in Mor and lowest in Mull (Fig. 2a). This clear differentiation highlights the differences in decomposition dynamics and organic matter accumulation, with slower turnover in Mor and highest in Mull (Baritz 2003). In contrast, carbon stocks in the mineral topsoil (0–5 cm) showed little variation among humus forms (Fig. 2b). The relative uniformity of mineral soil carbon stocks in the upper mineral soil (0–5 cm) can be explained by compensating physical, chemical, and biological processes. Along soil substrate gradients, nutrient-poor sites often have greater fine earth masses but lower carbon concentrations, whereas nutrient-richer, stony substrates contain less fine earth but higher carbon concentrations, resulting in similar total carbon stocks. Biological processes further influence vertical carbon redistribution: at Mull sites, bioturbation by soil fauna (e.g. earthworms) incorporates organic matter from the forest floor into the mineral soil, whereas at Mor sites, sharp organic–mineral boundaries indicate a partial decoupling between forest-floor carbon accumulation and stabilization in the mineral soil. Nevertheless, carbon transfer still occurs at these sites, particularly on sandy substrates, where podzolization facilitates the downward translocation of humic substances into deeper mineral horizons. Together, these compensatory mechanisms help explain why mineral soil carbon stocks remain relatively uniform across humus forms.

In contrast to carbon stocks, C:N ratios in the forest floor were similar across the three humus types (Fig. 2c), suggesting that early-stage decomposition and microbial processing tend to homogenize nutrient ratios despite differences in litter quality (Berg & Mcclaugherty 2020). In contrast, the mineral soil showed a clearer gradient in C:N ratios, with the highest values in Mor and the lowest in Mull (Fig. 2d), reflecting how parent material and nutrient cycling shape organic matter turnover and, ultimately, humus form development. Closely associated with these C:N patterns, soil chemical properties such as pH (Fig. 2e–f; Fig. 6a) and base saturation (Fig. 6b) also exert strong control on decomposition and humus form differentiation (Baritz 2003). Higher pH and base cation availability at Mull sites likely promote rapid litter breakdown and thinner organic layers, whereas acidic and base-poor conditions at Mor sites constrain decomposition and favor the accumulation of more recalcitrant organic matter. This contrast is mirrored in the soil buffering characteristics (Fig. 6f), with most Mull sites (88%) in the cation-exchange range and most Mor sites (62%) in the aluminum buffering range, highlighting that humus forms serve as clear indicators of soil pH and buffering status. These chemical controls are furthermore inherently linked to the parent material and soil substrate groups, which determine the nutrient supply and buffering capacity of a site. Nutrient-rich and well-buffered parent materials, such as limestone, basalt, and marl, favor rapid decomposition and Mull formation, whereas nutrient-poor or weakly buffered substrates, including sandy soils, shale, and Buntsandstein, generally support Moder or Mor humus forms (Tab. S4).

Beyond soil-related controls, both the dominant tree species and site moisture regime play a central role in organic matter decomposition and, consequently, humus form development. Deciduous tree species generally produce higher-quality litter that decomposes more rapidly and promotes the formation of Mull or Moder humus, whereas coniferous species (particularly spruce and pine) tend to produce more recalcitrant litter, favoring Moder or Mor humus forms (Baritz 2003; Tab. S3). Moisture conditions are arguably among the most important controls on organic matter decomposition (Berg & Mcclaugherty 2020), as oxygen availability governs the processes and communities underlying humus form development (Frank, Brauckmann & Broll 2023).

4.2 *Humus form transition dynamics and drivers of change*

Humus forms are dynamic and can change over time with shifting environmental conditions and associated decomposition processes. Over the past three decades, humus forms in northwest Germany have shifted markedly, in line with our hypothesis, toward types associated with faster organic matter turnover, with many sites transitioning from Mor to Moder or Mull, and also (but less frequently) from Moder to Mull and Mull to Moder (Fig. 3). These trajectories reflect different ecological processes that have occurred in forest ecosystems during this time. As the observed transitions parallel corresponding temporal trends in soil chemistry reported for the same monitoring points (Paar et al. 2016, Evers et al. 2019, 2022, Wellbrock & Bolte 2019), climate (IPCC 2022), and forest composition (Bundesministerium für Landwirtschaft, Ernährung und Heimat 2024), they are unlikely to result from observer bias or methodological inconsistency.

The observed changes in humus forms and forest-floor thickness reflect the combined and interacting influence of atmospheric deposition, soil chemistry, forest management, vegetation dynamics, and climate variability. The relative contribution of individual drivers is difficult to disentangle, as they act simultaneously and often interactively. Nitrogen deposition for example plays a complex role in organic matter decomposition. At low to moderate levels it can stimulate microbial activity and increase decomposition (Allison et al. 2009, Gill et al. 2022). Under chronic or elevated inputs, however, decomposition may slow due to shifts in litter chemistry toward more recalcitrant substrates, reduced production of lignin-degrading enzymes, and stoichiometric imbalances that lower microbial demand for nitrogen bound in organic matter (Aber et al. 1989, Zhu et al. 2015, Bowden et al. 2019, Berg & Mcclaugherty 2020). Evidence from German national-scale soil inventories supports this pattern, with sustained nitrogen deposition linked to reduced soil respiration and greater soil carbon storage (Grüneberg et al. 2019) and slower decomposition in nitrogen-rich forest floors (Fleck et al. 2019).

At the same time, forest-floor soil chemistry in northwestern Germany has generally improved following decades of acid deposition, as documented by regional forest soil inventories (Paar et al. 2016, Evers et al. 2019, 2022) and national assessments (Wellbrock & Bolte 2019). Reduced sulfur deposition, large-scale forest liming programs, and inputs of calcium-rich fly ash (in Saxony-Anhalt) have collectively enhanced nutrient availability and base saturation, creating conditions more favorable for decomposer activity and nutrient cycling (Fürst 2008, Evers et al. 2019, Meesenburg et al. 2019, van Straaten et al. 2023). These changes coincide with a shift in the Oh horizon from compact, fungal mycelium-bound structures to more granular and friable forms typical of Moder humus types. Forest management and vegetation change have further shaped humus dynamics. Namely, conversions from coniferous to deciduous stands improve litter quality, while practices such as thinning and selective cutting increase light availability and in turn soil surface temperatures and additionally promote natural regeneration, both of which enhance organic matter turnover (Prescott 2010, Wilcke et al. 2024).

Nevertheless, recent increases in forest-floor thickness (Fig. 5) suggest increasing constraints on decomposition, most likely due to more frequent and prolonged summer droughts (Werner & Matzner 2009) and sustained nitrogen deposition (Fleck et al. 2019, Grüneberg et al. 2019). While warming can enhance decomposition potential, water limitation during critical periods can offset favorable soil chemical conditions, leading to the accumulation of organic material. Conversely, in moist environments, episodic summer droughts may promote oxygen availability and even stimulate decomposition, potentially shifting organic matter dynamics toward humus forms with faster turnover. Climatic changes therefore exert a dual influence: with gradual warming enhancing decomposition potential while more frequent and prolonged droughts increasingly constrain it (Reichstein et al. 2013, Peñuelas et al. 2017).

However, the degree these climatic and deposition-related changes in soil chemistry affect the forest floor also depends on the properties of the underlying soil substrate (Labaz et al. 2014). The same drivers that accelerate decomposition on nutrient-poor, weakly buffered soils may have only muted effects on base-rich substrates. These effects were most pronounced on nutrient-poor or weakly buffered substrates such as Buntsandstein, sandy soils with little to no clay, or shales (Fig. 4 a-d). On these soils, limited base cation supply and inherently slow organic matter turnover made them especially sensitive to nitrogen deposition, warming, and vegetation change (Bowden et al. 2019). In contrast, soils formed on base-rich substrates such as basalt, diabase, marl, limestone, or loess loam (Fig. 4 e-h) showed relatively little change. Their high base saturation already supports rapid decomposition, leaving less potential for even further changes.

Consistent with these substrate effects, humus form changes can also be explained by differences in topsoil chemistry, particularly soil pH and base saturation (Fig. 6). Sites that transitioned to either Mull or Moder displayed distinctly different baseline soil chemistry than those that remained unchanged (either Mull or Moder, respectively). These findings suggest that humus form transitions, together with the associated shifts in litter decomposition and organic matter accumulation, represent dynamic processes closely linked to mineral soil chemistry. In contrast, transitions toward Mor (from Moder) showed no significant variation in mineral soil chemistry, further indicating that decomposition processes in these systems remain largely decoupled from the mineral soil.

Overall, humus form trajectories reflect the balance between processes that enhance decomposition and those that constrain it. Changes in soil chemical conditions, vegetation shifts toward higher-quality litter, forest management, and warming generally favor faster organic matter turnover, whereas drought stress, sustained high nitrogen inputs, and poor nutrient or moisture supply increasingly limit decomposition. The net direction of humus form development thus emerges from the interaction of these opposing influences, modulated by parent material, baseline soil chemistry, and site moisture regime.

4.3 Methodological considerations and sources of uncertainty

The asymmetry in observed transitions, with more Mor sites shifting to Moder than Moder sites to Mull, can be partly attributed to differences in the diagnostic criteria used to classify humus forms. Some transitions, such as from Mor to Moder, are relatively distinct, namely Mor horizons can be broken into intact pieces by hand, whereas Moder crumbles into smaller fragments (Wachendorf et al. 2023, Ad-hoc-Arbeitsgruppe Boden 2024). Because this distinction depends on the cohesiveness of the fermentation (Of) and humified (Oh) horizons, relatively small changes in biological activity, organic matter chemistry, or moisture can shift a site from one class to the other comparatively quickly, which likely contributes to the higher frequency of Mor-to-Moder transitions. In contrast, the Moder-to-Mull transitions are more gradual. Mull is defined by the absence of an Oh horizon, as litter here is rapidly decomposed and incorporated into the mineral soil by mesofauna and earthworms. Moder, by definition, retains an Oh horizon that can persist for decades, even under favorable decomposition conditions (Prescott 2010). Consequently, shifts between Moder and Mull require longer timescales, and are therefore less prevalent. Furthermore, humus forms can vary over short distances due to small differences in litter input, litter quality, moisture, and faunal activity (Aubert et al. 2006), adding another element of uncertainty to plot-level classifications.

Next, part of the variation observed across inventories may reflect differences in the classification systems themselves. Earlier inventories did not yet recognize humus forms at an initial stage of development (for instance, newly established forests on former agricultural land). In the updated KA6 classification system (Wachendorf et al. 2023, Ad-hoc-Arbeitsgruppe Boden 2024), such sites are explicitly recognized as “Initial,” but in earlier inventories such sites would have been assigned to another category that best fit the conditions present (if no Oh horizon was present then it would likely have been classified as Mull). In the third, and latest, NFSI Initial humus forms constituted 10% of the dataset, and because there was no direct equivalent category in earlier inventories, these sites were accordingly excluded in long-term comparisons, thereby reducing the sample size.

Lastly, a degree of uncertainty is also introduced by surveyor interpretation. Given that more than 30 years have passed since the first NFSI (in 1990), the training and calibration of the original surveyors is unclear, and some classifications, particularly of Mor humus forms in Hesse (Fig. S3), were possibly erroneous. We nevertheless retained all original records in the dataset, as we did not have any objective basis for excluding suspicious data.

5 Conclusions

The transition away from Mor toward Moder and Mull humus forms has significant ecological implications. From a nutrient perspective, the increasing prevalence of Moder and Mull is indicative of conditions associated with faster litter decomposition and higher nutrient mineralization rates, which are generally more conducive to tree growth and may enhance forest productivity. At the same time, with respect to carbon cycling, these humus form changes may be associated with increases in carbon turnover and stabilization processes; however, other constraints, particularly more frequent and prolonged summer droughts and sustained nitrogen deposition, appear to limit this process. From a soil chemistry perspective, the shift toward Moder and Mull reflects changes in soil chemical conditions following decades of sulfur-driven acidification, without implying an inherently beneficial trajectory among humus forms. Together these changes involve trade-offs between nutrient cycling and carbon retention, with implications for forest health, ecosystem functioning, and climate-mitigation considerations.

Changes in humus morphology also alter forest-floor thickness and water-holding capacity, affecting hydrology and possibly drought resilience. Our results support the hypothesis that humus forms in northwest Germany have shifted over the past three decades toward types associated with faster organic matter turnover. This shift reflects the combined effects of reduced acid deposition, elevated nitrogen inputs, liming programs, changing forest management, and climatic warming. Yet, the increasing frequency and intensity of summer droughts appear to counteract these decomposition-promoting factors by periodically constraining microbial activity and slowing litter breakdown.

Humus forms represent a sensitive and integrative indicator of environmental change, linking atmospheric inputs, soil chemistry, vegetation dynamics, and climate to ecosystem functioning. The shift toward Moder and Mull reflects substantial changes in forest-floor processes. Monitoring these dynamics not only confirms long-term changes in soil conditions but also provides insight into the trajectory of forest soil responses to environmental change.

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Supplementary

Tab. S1: Translation table of the different humus forms recorded in the three NFSI inventories. In the sixth edition of the German Soil Survey Guidelines (KA6) the definition of Mor humus forms was expanded to include what was previously Mor-like Moder humus forms.

Tab. S1: *Übersetzungstabelle der in den drei BZE-Inventuren erfassten Humusformen. In der sechsten Auflage der Bodenkundlichen Kartieranleitung (KA6) wurde die Definition von Rohhumus-Humusformen erweitert und umfasst nun Humusformen, die zuvor als „Rohhumusartiger Moder“ klassifiziert wurden.*

	NFSI I		**NFSI II**		**NFSI III**	
Type	**Methodology: NFSI 1 Code**		**KA5 Code**		**KA6 Code**	
Mull	MU	Mull	MU	Mull	M	Mull
					MLA	A-Mull
	MUT	Typical L-Mull	MUT	Typical L-Mull	MLT	Typical L-Mull
					MLF	Moist L-Mull
	MUF	F-Mull	MUO	F-Mull	MF	F-Mull
					MFL	L Mull-like F Mull
					MFT	Typical F-Mull
					MFM	Moder-like F-Mull
	AMU	Moist Mull	MUF	Moist Mull	MFF	Moist F-Mull
					MFR	Rhizo-F-Mull
Moder	MOU	Mull-like Moder	MOM	Mull-like Moder	AMM	Mull-like Moder
	MOT	Typical Moder	MOT	Typical Moder	AMT	Typical Moder
	MOTA	Typical Moder *(poor in fine OM)*	MOA	Typical Moder *(poor in fine OM)*	AMTA	Typical Moder *(poor in fine OM)*
	MOTR	Typical Moder *(rich in fine OM)*	MOR	Typical Moder *(rich in fine OM)*	AMTR	Typical Moder *(rich in fine OM)*
			MOF	Moist-Moder	AMF	Moist –Moder
	SHGM	Rhizo-Moder	GMO	Rhizo-Moder	AMR	Rhizo-Moder
			TA	Tangel	AMA	Tangel
	MOR	Mor-like Moder	MR	Mor-like Moder	ARM	Moder-like Mor
	MOROAR	Mor-like Moder *(poor in fine OM)*	MRA	Mor-like Moder *(poor in fine OM)*	ARMA	Moder-like Mor *(poor in fine OM)*
	MOROREI	Mor-like Moder *(rich in fine OM)*	MRR	Mor-like Moder *(rich in fine OM)*	ARMR	Moder-like Mor *(rich in fine OM)*
Mor	ROT	Typical Mor	ROT	Typical Mor	ART	Typical Mor
	ROTA	Typical Mor *(poor in fine OM)*	ROA	Typical Mor *(poor in fine OM)*	ARTA	Typical Mor *(poor in fine OM)*
	ROTR	Typical Mor *(rich in fine OM)*	ROR	Typical Mor *(rich in fine OM)*	ARTR	Typical Mor *(rich in fine OM)*
	ARO	Moist Mor	ROF	Moist Mor	ARF	Moist Mor
Initial*					IM	Initial Mull
					IA	Initial humus form with organic surface layers
Degraded*					XH	Naturally degraded
					XR	Anthropogenically degraded

* Initial and degraded humus form types were only introduced in the sixth edition of the German Soil Survey Guidelines (KA6). Accordingly, there is no equivalent humus form in the first two inventories.

Tab. S2: Plot counts of the humus form types found in the four federal states respectively and overall, for northwest Germany. Percentages refer to the proportion within each federal state and inventory. The two plots in Hamburg were combined with those in Schleswig Holstein, and the four plots in Bremen were combined with those in Lower Saxony.

Tab. S2: *Flächenanzahlen der Humusformtypen in den jeweiligen Bundesländern sowie insgesamt für Nordwestdeutschland. Prozentwerte beziehen sich auf den Anteil innerhalb des jeweiligen Bundeslandes und der jeweiligen Inventur. Die zwei Flächen in Hamburg wurden mit Schleswig-Holstein zusammengefasst, die vier Flächen in Bremen mit Niedersachsen.*

Federal state and humus form	**NFSI I**	**NFSI II**	**NFSI III**
Lower Saxony	204	167	185
Mull	32 (16%)	34 (20%)	40 (22%)
Moder	126 (62%)	109 (65%)	101 (55%)
Mor	46 (23%)	24 (14%)	15 (8%)
Initial *	n.a.	n.a.	29 (16%)
Hesse	139	136	143
Mull	52 (37%)	60 (44%)	51 (36%)
Moder	84 (60%)	56 (41%)	77 (54%)
Mor	3 (2%)	20 (15%)	13 (9%)
Initial *	n.a.	n.a.	1 (1%)
Degraded *	n.a.	n.a.	1 (1%)
Saxony-Anhalt	63	74	94
Mull	5 (8%)	18 (24%)	22 (23%)
Moder	25 (40%)	41 (55%)	60 (64%)
Mor	33 (52%)	15 (20%)	3 (3%)
Initial *	n.a.	n.a.	9 (10%)
Schleswig-Holstein	41	37	43
Mull	7 (17%)	9 (24%)	12 (28%)
Moder	15 (37%)	15 (41%)	16 (37%)
Mor	19 (46%)	13 (35%)	8 (19%)
Initial *	n.a.	n.a.	7 (16%)
∑ Northwest Germany	447	414	465
Mull	96 (21%)	121 (29%)	125 (27%)
Moder	250 (56%)	221 (53%)	254 (55%)
Mor	101 (23%)	72 (17%)	39 (8%)
Initial *	n.a.	n.a.	46 (10%)
Degraded *	n.a.	n.a.	1 (0%)

* Initial and degraded humus form types were only introduced in the sixth edition of the German Soil Survey Guidelines (KA6). Accordingly, there is no equivalent humus form in the first two inventories.

Tab. S3: Distribution of humus form types across different substrate groups in the third NFSI. The substrate groups are broadly sorted based on soil fertility from substrates with low base saturations to high base saturations. Percentages indicate the proportion for each respective substrate group.

Tab. S3: *Verteilung der Humusformtypen auf verschiedene Substratgruppen in der BZE III. Die Substratgruppen sind grob nach Bodenfruchtbarkeit von niedriger zu hoher Basensättigung geordnet. Prozentwerte geben den Anteil innerhalb der jeweiligen Substratgruppe an.*

Base saturation category	Substrate	Mull	Moder	Mor	Initial	Degraded	Number of plots
Low base saturation	Granite	-	2 (67%)	1 (33%)	-	-	3
	Quartzite	-	4 (80%)	1 (20%)	-	-	5
	Sand, no silt or clay	9 (8%)	73 (68%)	9 (8%)	16 (15%)	-	107
	Buntsandstein	10 (25%)	25 (63%)	4 (10%)	-	1 (3%)	40
	Shale	6 (24%)	17 (68%)	2 (8%)	-	-	25
	∑ Substrates with low base saturation	25 (14%)	121 (67%)	17 (9%)	16 (9%)	1 (1%)	180
Medium base saturation	Organic	1 (10%)	6 (60%)	3 (30%)	-	-	10
	Cretaceous sandstone	-	2 (67%)	1 (33%)	-	-	3
	Sand, slightly loamy	1 (3%)	27 (73%)	3 (8%)	6 (16%)	-	37
	Loess loam	18 (43%)	22 (52%)	1 (2%)	1 (2%)	-	42
	Sand, loamy	4 (33%)	3 (25%)	4 (33%)	1 (8%)	-	12
	Greywacke	3 (21%)	9 (64%)	2 (14%)	-	-	14
	Claystone	8 (80%)	1 (10%)	1 (10%)	-	-	10
	Loam	9 (69%)	4 (31%)	-	-	-	13
	∑ Substrates with medium base saturation	44 (31%)	74 (52%)	15 (11%)	8 (6%)	0 (0%)	141
High base saturation	Marl	4 (36%)	5 (45%)	1 (9%)	1 (9%)	-	11
	Zechstein	1 (33%)	2 (67%)	-	-	-	3
	Basalt/Diabase	11 (65%)	5 (29%)	-	1 (6%)	-	17
	Limestone	14 (78%)	4 (22%)		-	-	18
	∑ Substrates with high base saturation	30 (61%)	16 (33%)	1 (2%)	2 (4%)	0 (0%)	49

Tab. S4: Total number of plots categorized by humus form types across different forest types in the second National Forest Soil Inventory (NFSI). Percentages indicate the proportion for each respective forest type.

Tab. S4: *Gesamtzahl der Flächen nach Humusformtypen in verschiedenen Bestockungstypen in der zweiten Bodenzustandserhebung im Wald (BZE II). Prozentangaben beziehen sich auf den Anteil innerhalb des jeweiligen Bestockungstyps.*

Forest composition	Mull	Moder	Mor
Beech > 70%	41 (55%)	32 (43%)	1 (1%)
Oak > 70%	15 (71%)	5 (24%)	1 (5%)
Other deciduous tree types > 70 %	27 (73%)	8 (22%)	2 (5%)
Mixed deciduous forest < 30 % conifer	2 (25%)	6 (75%)	-
Mixed deciduous forest > 30 % conifer	13 (54%)	7 (29%)	4 (17%)
∑ Deciduous	98 (60%)	58 (35%)	8 (5%)
Pine > 70 %	9 (7%)	85 (70%)	28 (23%)
Spruce > 70 %	3 (5%)	36 (57%)	24 (38%)
Mixed coniferous tree types > 70%	2 (7%)	20 (71%)	6 (21%)
Mixed coniferous forest < 30% deciduous forest	1 (25%)	3 (75%)	-
Mixed coniferous forest > 30% deciduous forest	6 (22%)	16 (59%)	5 (19%)
∑ Coniferous	21 (11%)	160 (86%)	5 (3%)

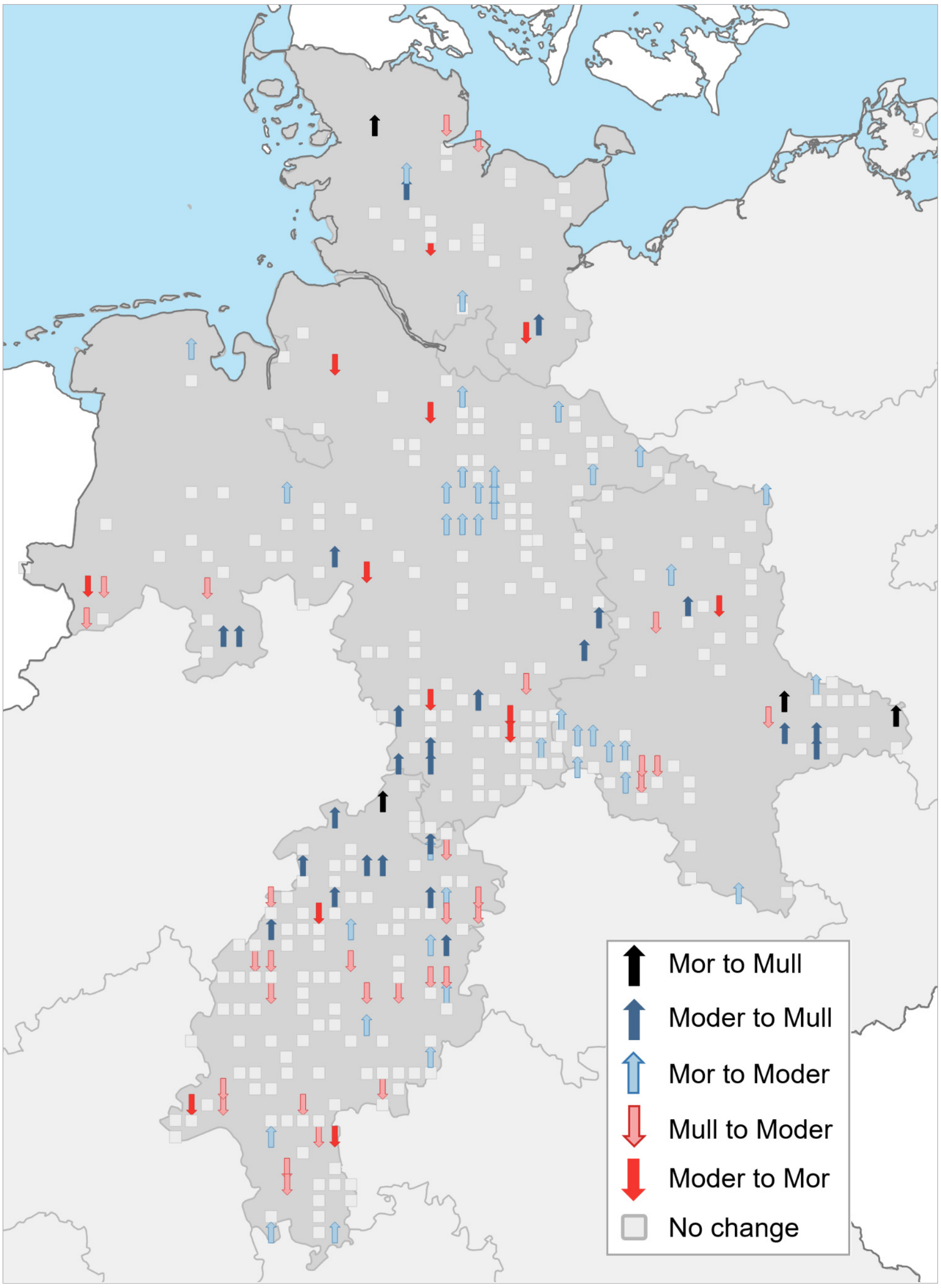

Fig. S1: Changes in humus form types between the second (2006) and third NFSI (2023).

Abb. S1: *Veränderungen der Humusformtypen zwischen der zweiten (2006) und dritten BZE (2023).*

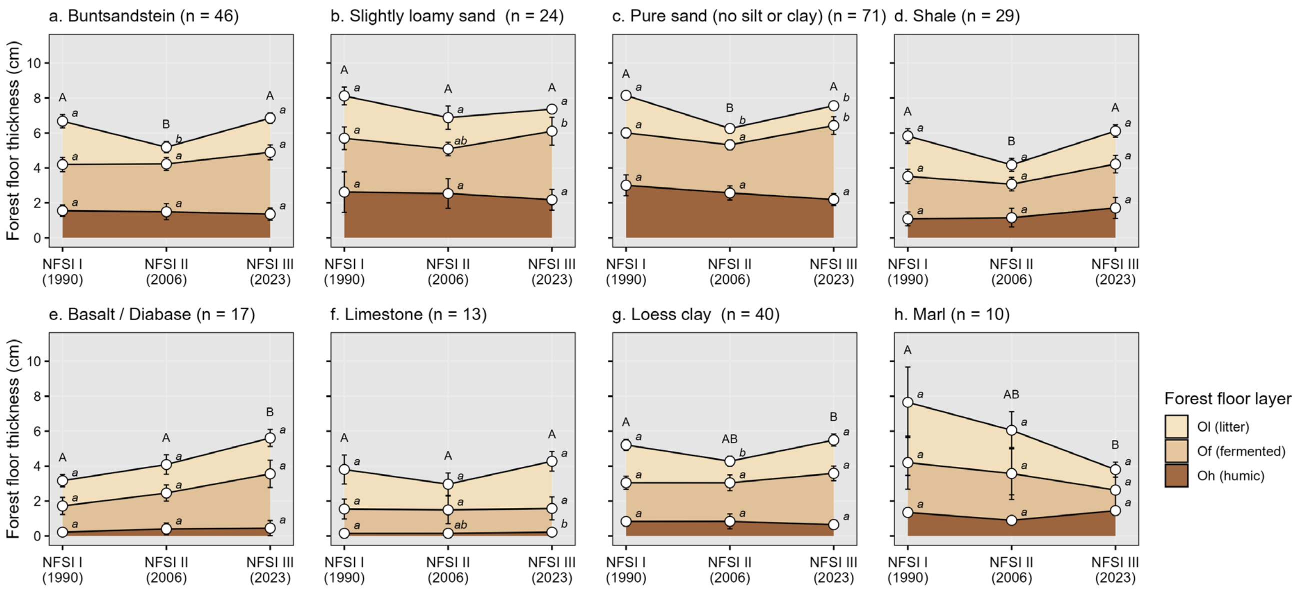

Fig. S2: Stacked area plots showing mean thickness of forest floor layers (L – litter, Of – fermented, Oh – humic) across the three NFSI inventories for four nutrient-poor soil substrate groups (a. Buntsandstein, b. Slightly loamy sand, c. Pure sand, d. Shale) and four nutrient-rich soil substrate groups (e. Basalt/Diabase, f. Limestone, g. Loess clay, h. Marl). Error bars represent 95% confidence intervals. Lowercase letters indicate statistically significant differences between inventories for individual layers (pairwise Wilcoxon tests, α = 0.05). Uppercase letters indicate differences in total forest-floor thickness.

Abb. S2: *Gestapelte Flächendiagramme der mittleren Mächtigkeit der Auflagehorizonte (L – Streu, Of – Fermentation, Oh – Humus) über die drei BZE-Inventuren für vier nährstoffarme Substratgruppen (a. Buntsandstein, b. schwachverlehmter Sand, c. unverlehmter Sand, d. Tonschiefer) und vier nährstoffreiche Substratgruppen (e. Basalt/Diabas, f. Kalkstein, g. Lösslehm, h. Mergel). Fehlerbalken zeigen 95%-Konfidenzintervalle. Kleinbuchstaben kennzeichnen signifikante Unterschiede zwischen Inventuren für einzelne Horizonte (paarweise Wilcoxon-Tests, α = 0.05). Großbuchstaben kennzeichnen Unterschiede in der Gesamtmächtigkeit der Auflage.*

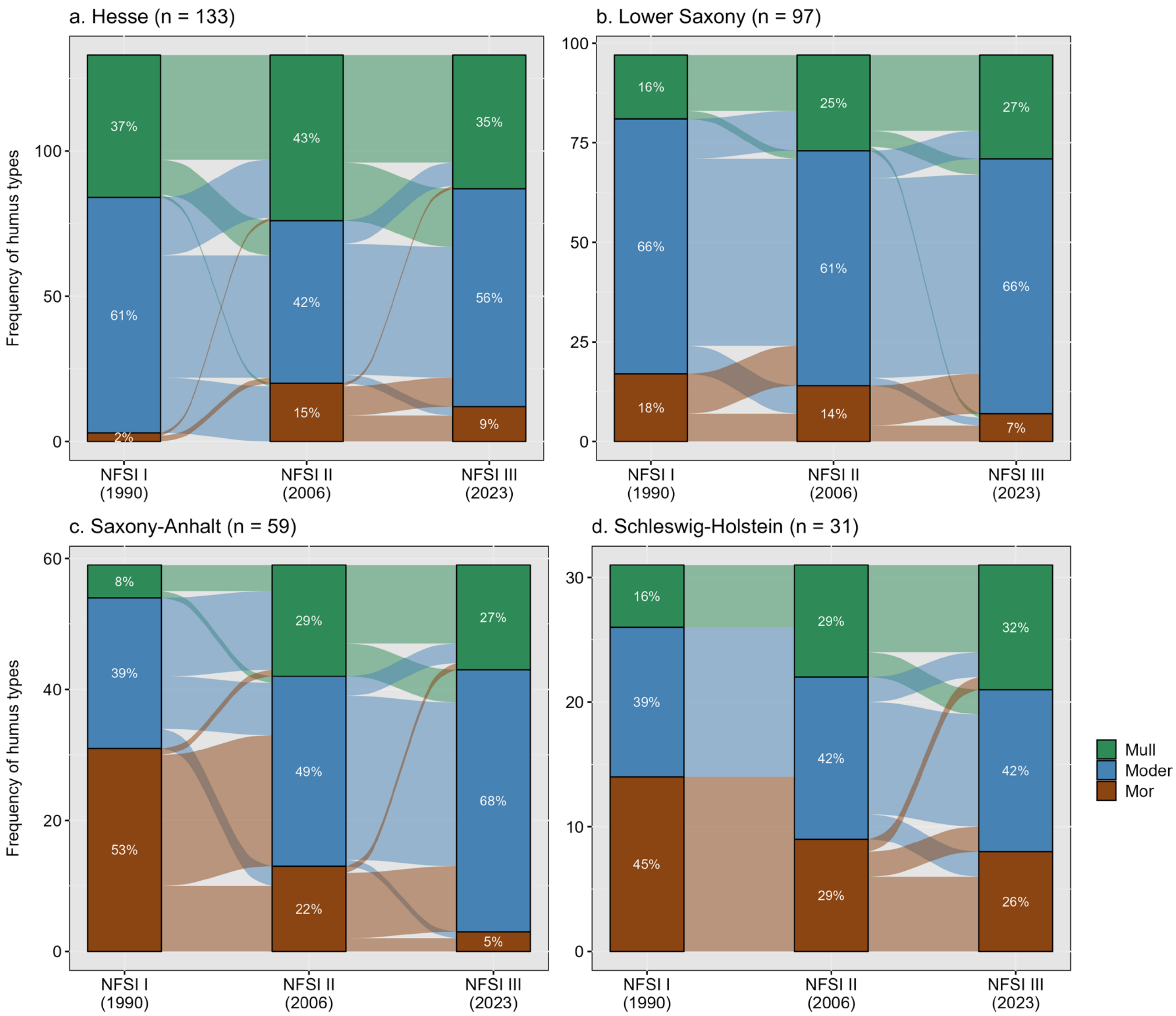

Fig. S3: Sankey diagram showing the development of humus forms across three forest soil inventories (NFSI I, II, III) for four German federal states: Hesse, Lower Saxony, Saxony-Anhalt, and Schleswig-Holstein. The width of the flows indicates the number of plots transitioning between humus types, with percentages showing relative frequency within each stratum. The NFSI points in Hamburg (n = 2) were included with the Schleswig-Holstein data, and the data from Bremen (n = 4) were combined with that of Lower Saxony.

Abb. S3: *Sankey-Diagramm zur Entwicklung der Humusformentypen über drei BZE-Inventuren (BZE I, II, III) in vier Bundesländern: Hessen, Niedersachsen, Sachsen-Anhalt und Schleswig-Holstein. Die Breite der Flüsse entspricht der Anzahl der Flächen mit Übergängen zwischen Humustypen; Prozentwerte geben die relativen Häufigkeiten innerhalb der jeweiligen Strata an. BZE-Punkte in Hamburg (n = 2) wurden Schleswig-Holstein zugeordnet; Daten aus Bremen (n = 4) wurden mit Niedersachsen zusammengefasst.*