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Drastic herb layer decline in european beech forests: evidence from the Steigerwald (Germany) under climate-related drought despite close-to-nature forestry

Drastischer Rückgang der Krautschicht in Buchenwäldern: Ergebnisse aus dem Steigerwald (Bayern) unter klimabedingtem Trockenstress trotz naturnaher Bewirtschaftung

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Abstract

This study investigates long-term changes in the structure and species composition of deciduous forests in the Steigerwald, southern Germany, managed under close-to-nature forestry principles for over five decades. In 2016, we resurveyed 151 phytosociological relevés, initially conducted between 1980 and 1982, to evaluate shifts in forest dynamics over a 30-year period. We focused on beech (Fagus sylvatica), *oak-hornbeam* (Carpinus betulus), *and oak (*Quercus spp.*) forest types, recognized for their biodiversity and natural regeneration capacity.*

We observed a substantial decline in herb layer cover from a median of 55% to 16%. This reduction could not be fully attributed to increased canopy shading, as tree and shrub cover explained only 4% of the variation, while the year of sampling (observation period) accounted for 23%. Most species indicated intermediate moisture conditions. The decline affected species with low as well as high nitrogen and light indicator values. These patterns suggest that drought, likely driven by climate change, played a major role in the herb layer's decline.

We recorded 274 understory species, with 28% showing significant changes in cover. Although species richness and evenness per plot remained constant, species composition became less diverse, and strong fluctuations occurred in the understory. In contrast, the overstory exhibited minimal changes, indicating that the most pronounced shifts in vegetation structure took place in the herbaceous layer.

Climatic data of the Steigerwald region revealed considerable environmental changes during the study period: mean annual temperatures increased from 7.3 °C in 1963 to 9.0 °C in 2021, with more warm summer days and fewer frost days. A severe water balance deficit of -220 mm in 2015, relative to the long-term mean (1995–2022), underscores the escalating drought stress on the ecosystem. These climatic changes likely contributed to the decline of moisture-sensitive understory species.

*Although close-to-nature forest management practices, like selective harvesting and natural regeneration, were successful in preserving the species composition of the overstory, they had limited impact on the herb layer, where climate-related stressors dominated. Crown thinning created through management, though increasing light availability, may also accelerate forest floor drying and intensify drought impacts on the herb layer. Potential natural vegetation (PNV) models, based on climate and soil data, project that rising temperatures will shift habitat conditions from beech-dominated forests (*Galio-Fagetum*) to more drought-resistant hornbeam-oak forests (*Galio-Carpinetum*). We recommend that forest managers expand close-to-nature strategies to better support forest floor vegetation, integrating long-term monitoring and water retention measures to enhance forest resilience in the face of climate change. Moreover, it would be valuable to examine how changes in the herb layer affect insects and other animals that rely on this vegetation for habitat and food, providing a more complete ecological understanding.*

Keywords*: Deciduous forests, Herb layer decline, Species composition shifts, Close-to-Nature Management, Long-Term Monitoring, Drought Stress*

Erweiterte deutschsprachige Zusammenfassung

Einführung

Die EU-Waldstrategie 2030 fördert die naturnahe Waldbewirtschaftung, um Biodiversität und Anpassungsfähigkeit von Wäldern an den Klimawandel zu stärken (Bauhus et al. 2013, Larsen et al. 2022, Krumm et al. 2023). Im Steigerwald, geprägt durch Buchen-, Eichen- und Eichen-Hainbuchenwälder, wird

seit über fünf Jahrzehnten nach diesen Prinzipien gewirtschaftet (BaySF 2017, Mergner 2018, Mergner & Kraus 2020). Diese Studie untersucht langfristige Veränderungen der Vegetationsstruktur und Artendynamik zwischen den Jahren 1980–1982 und 2016, um die Auswirkungen naturnaher Bewirtschaftung auf die Struktur und Diversität der Waldökosysteme zu analysieren.

Die zentralen Fragestellungen sind:

- Wie haben sich die Vegetationsschichten entwickelt?
- Welche Veränderungen gibt es im Artenreichtum und in der Zusammensetzung von Ober- und Unterwuchs?
- Welchen Einfluss haben Bewirtschaftungspraktiken, insbesondere auf die Bodenvegetation?
- Welche Umweltfaktoren erklären die starken Veränderungen im Unterwuchs?

Untersuchungsgebiet

Die Untersuchungsflächen liegen im Steigerwald, einem Mittelgebirge in Bayern mit Höhenlagen bis zu 498 m ü. NN. Die Böden bestehen aus einem Mosaik toniger, lehmiger und sandiger Substrate des Unteren und Mittleren Keupers. Historisch wandelte sich die Waldnutzung von Niederwald im 17. und 18. Jahrhundert hin zu Buchen-Hochwald im 19. Jahrhundert. Seit Mitte des 20. Jahrhunderts wird der Steigerwald naturnah bewirtschaftet, wobei Einzelstammentnahmen und natürliche Verjüngung den Buchenanteil erhalten und die Resilienz der Wälder stärken sollen (Mergner & Kraus 2020). Dabei verbindet der Steigerwald Holznutzung mit Biodiversitätsschutz, um stabile und anpassungsfähige Waldökosysteme zu fördern. Die Waldzusammensetzung besteht zu 73 % aus Laubbäumen, dominiert von Buche (40 %) und Traubeneiche (21 %), während Nadelbäume 27 % ausmachen, überwiegend Kiefer (15 %), Fichte (7 %) und Lärche (4 %). Der Holzvorrat beträgt 388 m³/ha bei einem jährlichen Wachstum von 10,8 m³/ha, wovon 70 % genutzt werden. 12% der Fläche sind aus der Nutzung genommen.

Die vorherrschende Waldtypen umfassen Luzulo-Fagetum, Galio odorati-Fagetum, Luzulo-Quercetum und Galio-Carpinetum (Rennwald 2000, Welss 1985).

Methoden

Felderhebung: Zwischen 1980 und 1982 führte Walter Welß eine umfassende Erhebung der Waldvegetation im Steigerwald durch, bei der über 500 pflanzensoziologische Aufnahmen erstellt wurden (Welss 1985). 2016 wurden 151 dieser Flächen in Buchen- und Buchenmischwäldern erneut untersucht. Die Vegetation wurde in fünf Schichten unterteilt: obere und untere Baumschicht, Strauchschicht, Krautschicht und Moosschicht. Zur Dokumentation der Bewirtschaftungsgeschichte wurden Baumstümpfe erfasst, deren Anzahl gezählt und der Zerfallsgrad in fünf Stufen klassifiziert, um Rückschlüsse auf den relativen Zeitpunkt und die Intensität vergangener Holznutzungen zu ziehen.

Analyse der Schichten: Die statistische Auswertung erfolgte in R (Version4.2.2). Die Deckung der Vegetationsschichten (Baumschicht, Strauchschicht, Krautschicht) wurde aus der Deckung der vorkommenden Arten berechnet. Veränderungen in den Schichten wurden mithilfe von Wilcoxon-Tests auf Signifikanz geprüft. Regressionsanalysen dienten der Untersuchung des Zusammenhangs zwischen der Gehölzschicht und der Krautschicht.

Dynamik der Artenzusammensetzung: Änderungen in der Artenzusammensetzung wurden für die Baum- und Krautschicht separat untersucht. Die Visualisierung dieser Veränderungen erfolgte durch Korrespondenzanalysen (CA). Zur detaillierten Analyse kamen Cluster- und Diskriminanzanalysen zum Einsatz, um spezifische Verschiebungen innerhalb der Baum- und Krautschicht zu erfassen. Verschiebungen der Waldtypen wurden anschaulich durch Sankey-Diagramme dargestellt.

Nutzungshistorie: Anhand der Baumstümpfe auf den Probeflächen, deren Anzahl als Maß für die Nutzungsintensität und deren Zerfallsgrad als Indikator für den relativen Zeitpunkt der Holzentnahme dienten, wurden die Flächen mittels Clusteranalyse in vier Gruppen klassifiziert.

Haupttreiber der floristischen Veränderungen:

Zur Identifizierung der Hauptfaktoren für die floristischen Veränderungen wurden Vegetationsdaten, Wetteraufzeichnungen (1963–2019) und Daten zur potenziellen natürlichen Vegetation (PNV) von Bayern (Fischer et al. 2019) herangezogen. Umweltfaktoren wie Licht- und Stickstoffverfügbarkeit wurden durch Ellenberg-Zeigerwerte quantifiziert. Die Analyse von Klimakennwerten, wie die mittlere Jahrestemperatur, die absolute Tiefsttemperatur und die absolute Höchsttemperatur, die Anzahl der Eis- und Frost-, Sommer- und Hitzetage gibt Aufschluss über die langjährige Entwicklung der Wetterbedingungen. Die Waldgesellschaften der aktuellen und zukünftigen PNV-Modellierung von Bayern wurden für die Aufnahmepunkte bestimmt. Veränderungen in der Vegetation wurden als Sankey-Diagramme und Karten visualisiert, um standörtliche und räumliche Muster deutlich zu machen.

Ergebnisse

Gesamtdeckung der Schichten (Abb.1): Zwischen 1985 und 2016 sank die Deckung der oberen Baumschicht von 62 % auf 52 %, während die untere Baumschicht von 17 % auf 27% anstieg. Die Krautschicht verringerte sich drastisch von 55 % auf 16 %. Die Gehölzschicht stieg leicht von 68 % auf 72 %. Zwei bivariate Regressionsanalysen zeigen (Abb. 2), dass die Krautschicht 1985 nur schwach durch die Beschattung der Gehölzschicht beeinflusst wurde ($p = 0,04$, $R^2 = 2\%$). Im Jahr 2016 bestand kein signifikanter Zusammenhang zwischen der Deckung der Gehölzschicht und der Deckung der Krautschicht. Jedoch liegt die Regressionsgerade 1985 deutlich höher als 2016. Das bedeutet, dass ein anderer Faktor als die Deckung der Gehölze, der sich von 1985 nach 2016 verändert hat, diesen Rückgang verursacht haben muss. Dieser Faktor erklärt 24 % der Variabilität der Deckung der Krautschicht.

Dynamik der Arten: 77 von 286 Arten (Mehrfachnennung der Baumarten in verschiedenen Schichten) veränderten ihre Deckung signifikant, 21 nahmen im Unterwuchs zu, während 55 abnahmen. Die Naturverjüngung in der Strauch- und Krautschicht hat an Diversität gewonnen, da mittlerweile eine größere Vielfalt an Arten vertreten ist als zuvor. Besonders auffällig war der Rückgang spezialisierter Krautschichtarten wie *Luzula luzuloides* und *Galium odoratum,* die für Buchenwälder charakteristisch sind. Generalisten wie *Rubus fruticosus* und *Urtica dioica* hingegen nahmen zu. In der

Baumschicht nahm nur die Deckung von *Sorbus torminalis* signifikant zu (Anhang 2).

Artenreichtum und Gleichverteilung: In 302 Aufnahmen (je 151 zu den beiden Aufnahmezeitpunkten) wurden insgesamt 194 Arten in der Krautschicht (ohne Naturverjüngung) erfasst. Der Artenreichtum und die Gleichverteilung zeigen keine signifikanten Unterschiede zwischen 1985 und 2016 (Abb.3).

Veränderungen der Baumschicht: Die Artzusammensetzung und die Deckung der Baumschicht zeigt kaum Veränderungen (Abb. 5, Abb. 6).

Veränderung der Krautschicht: Die Korrespondenzanalyse (Abb. 4) weist auf eine Homogenisierung der Krautschicht hin. Die Dynamik der Vegetationsveränderungen wird durch ein Sankey-Diagramm anschaulich dargestellt (Abb. 11). Die Darstellung erleichtert die Identifikation sowohl von unveränderten Waldtypen als auch von solchen mit signifikanten Umstrukturierungen sowie das Verständnis der Entstehung neuer Waldtypen. Einige Waldtypen der basenarmen Buchenwälder und Eichen-Hainbuchenwälder blieben weitgehend unverändert, während andere erhebliche Veränderungen erfuhren oder vollständig verschwanden. Besonders anfällig für Veränderungen im Unterwuchs sind Buchenwälder auf basenreichen Böden. Nähere Informationen zu den Veränderungen sind in Anhang 2 und 3 zu finden.

Nutzungshistorie: Die vier Gruppen, die durch unterschiedliche Durchforstungsgrade charakterisiert sind, weisen floristisch nur geringe Unterschiede auf. Weder im Artenreichtum noch in der Gleichverteilung oder der Deckung der Baum-, Strauch- und Krautschicht konnten zwischen den Gruppen signifikante Veränderungen festgestellt werden.

Haupttreiber der Veränderungen: Der Rückgang der Krautschicht weist auf signifikante Veränderungen der Standortbedingungen hin. Die Analyse der mittleren Ellenberg-Zeigerwerte zeigte jedoch keine wesentlichen Änderungen, mit Ausnahme eines leichten Anstiegs der Stickstoffzahl von 4,7 auf 5,0. Die Spektren der Lichtzahl verdeutlichen, dass sowohl schattentolerante als auch lichtliebende Pflanzen zurückgegangen sind. Schattentolerante Arten nahmen nicht zu, was mit der nur geringfügigen Zunahme der Gehölzdeckung übereinstimmt. Die Deckung von Arten mit hohen oder niedrigen Stickstoffzeigerwerten blieb entweder konstant oder ging zurück, eine Zunahme der Deckung stickstoffliebender Arten wurde nicht festgestellt (Abb. 13). Alle Raunkiaer-Lebensformen verzeichneten einen Rückgang, besonders ausgeprägt bei Hemikryptophyten (Abb. 14). Klimadaten aus der Region dokumentieren eine Erwärmung um 2,9 K pro Jahrhundert (Abb. 15, Appendix 5). PNV-Modelle prognostizieren eine zunehmende Dominanz von Galio-Carpinetum-Gesellschaften (Abb. 16, Abb. 17).

Diskussion

Die beobachtete Zunahme der unteren Baumschicht und der Strauchschicht sowie der Rückgang der Krautschicht entsprechen Trends, die auch in anderen Regionen festgestellt wurden. Im Steigerwald jedoch ist die Reduktion der Krautschicht besonders drastisch, während die Zunahme der Gehölze moderat bleibt.

Die Analyse der Ellenberg-Zeigerwerte zeigt, dass sowohl lichtliebende als auch schattentolerante Arten in ihrer Deckung zurückgegangen sind. Diese Ergebnisse deuten darauf hin, dass Veränderungen der Lichtverhältnisse für die Änderungen in der Bodenvegetation nur eine untergeordnete Rolle spielen. Auffällig ist der Rückgang der Hemikryptophyten, der nicht allein durch die moderate Zunahme der Gehölzdeckung erklärt werden kann. Stattdessen scheinen klimatische Faktoren wie Temperaturanstieg und Trockenheit eine entscheidende Rolle zu spielen. Dürreereignisse, insbesondere im Jahr 2015, bieten die plausibelste Erklärung für den drastischen Rückgang der Biomasse in der Krautschicht. Daten der bayerischen Waldklimastation Ebrach belegen eine extreme negative Abweichung der klimatischen Wasserbilanz (-220 mm) vom langjährigen Mittel (1995–2022) sowie eine deutliche Kronenausdünnung bei Buchen, die 43 % ihres Laubwerks verloren. Die Kronenausdünnung führt zwar zu helleren Bedingungen und damit besseren Voraussetzungen für Photosynthese. Sie könnte aber auch zu stärkerer Verdunstung, zu trockeneren Bedingungen geführt haben, die das Wachstum vieler Pflanzen erschwerten. Die Artenzusammensetzung und die Deckung der Baumschichten blieben weitgehend unverändert, abgesehen vom Rückgang standortfremder Nadelgehölze – ein erklärtes Ziel der naturnahen Forstwirtschaft. Die naturnahe Forstwirtschaft hat erfolgreich Verbißschäden durch Wild begrenzt und eine artenreiche Naturverjüngung gefördert. Diese Maßnahmen können jedoch nicht den drastischen Rückgang der Biomasse in der Krautschicht erklären.

Die Artenzahl und ihre Gleichverteilung (Evenness) blieben trotz der Biomasseverluste in der Krautschicht konstant, was darauf hinweist, dass die Biodiversität bislang erhalten ist. Die numerische Klassifikation zeigt, dass 2016 im Wesentlichen dieselben Pflanzengesellschaften vertreten sind wie bei der Erhebung von Welss (1985). Dennoch wurden signifikante Veränderungen in der Artenzusammensetzung festgestellt, insbesondere beim Galio-Fagetum (Buchenwälder auf basenreichen Böden), das Anzeichen einer Umstrukturierung aufweist. Gleichzeitig sind bodensaure Gesellschaften seltener geworden, was auf eine Erholung von den Auswirkungen des sauren Regens hindeuten könnte.

Untersuchungen zur Bewirtschaftungshistorie zeigen, dass alle Nutzungstypen vom Rückgang der Krautschicht betroffen sind. Kronenauflichtungen, die die Naturverjüngung fördern sollen, haben grundsätzlich positive Effekte auf die Krautschicht. Unter trockenen Bedingungen könnten sie jedoch die Verdunstung am Boden erhöhen und dadurch die Wasserversorgung der Waldbodenpflanzen gefährden.

Trotz erheblicher Nährstoffeinträge aus der Luft ist lediglich ein geringer Anstieg der mittleren Stickstoffzahl festzustellen, während die Biomasse der Krautschicht nicht zugenommen hat, sondern zurückgegangen ist. Dies ist möglicherweise eine Folge der limitierten Wasserverfügbarkeit.

Simulationen der potenziellen natürlichen Vegetation (PNV) zeigen, dass eine Erhöhung der mittleren Jahrestemperatur, Temperaturerhöhung von 1 °C, zu einer Verschiebung von Buchenwäldern hin zu Eichen-Hainbuchenwäldern führen könnte, die mit geringerer Wasserverfügbarkeit besser zurechtkommen.

Schlussfolgerungen

Die mangelnde Wasserverfügbarkeit spielt eine zentrale Rolle für die beobachteten Veränderungen in der Krautschicht und

die langfristige Resilienz des Waldökosystems. Der dokumentierte Temperaturanstieg von 1985 bis 2016 und die extreme Dürre im Jahr 2015 haben die klimatische Wasserbilanz erheblich verschlechtert. Insbesondere die Krautschicht, deren Wurzeln oft in oberflächennahen Bodenschichten liegen, ist von Trockenstress stark betroffen. Der Rückgang der Biomasse und die Stagnation der Naturverjüngung können direkt mit der limitierten Wasserverfügbarkeit in Verbindung gebracht werden. Zwar haben Kronenauflichtungen, die für die Förderung der Naturverjüngung eingesetzt werden, kurzfristig positive Effekte auf die Lichtverhältnisse, unter trockenen Bedingungen verstärken sie jedoch die Bodenverdunstung und verschärfen somit den Wassermangel.

Trotz erheblicher Nährstoffeinträge aus der Luft (z. B. Stickstoffdepositionen) ist lediglich ein geringer Anstieg der mittleren Stickstoffzahl festzustellen, während die Biomasse der Krautschicht weiter zurückgeht. Der Rückgang von lichtliebenden und schattentoleranten Arten zeigt zudem, dass eine Veränderung der Lichtverhältnisse keine entscheidende Rolle spielt. Dies deutet darauf hin, dass Nährstoffverfügbarkeit den Wasserstress nicht kompensieren kann. Simulationen der potenziellen natürlichen Vegetation (PNV) zeigen, dass zunehmende Trockenheit langfristig zu einer Verschiebung von Buchenwäldern hin zu trockenheitstoleranteren Arten wie Eichen und Hainbuchen führen könnte.

Um den Herausforderungen des Klimawandels zu begegnen, sind angepasste Managementstrategien notwendig. Maßnahmen wie die Förderung tiefer wurzelnder Arten, der Erhalt der Bodenfeuchtigkeit durch Bodenbedeckung oder eine gezielte Kronenpflege könnten dazu beitragen, die Wasserverfügbarkeit zu verbessern. Die Konstanz der Artenvielfalt in der Krautschicht verdeutlicht, dass die Biodiversität derzeit noch erhalten ist. Sie muss jedoch aktiv gefördert werden, um die Anpassungsfähigkeit des Waldökosystems langfristig zu sichern.

Die nachhaltige Forstwirtschaft im Steigerwald hat positive Effekte auf die Naturverjüngung und die Erhaltung der Biodiversität gezeigt. Angesichts zunehmender Trockenheit und Wasserstress reichen diese Maßnahmen jedoch nicht aus, um die Krautschicht und das gesamte Waldökosystem zukunftssicher zu machen. Neben der proaktiven Förderung trockenheitstoleranter Arten wie Eiche und Hainbuche sollten gezielte Maßnahmen zur Verbesserung der Wasserhaltefähigkeit des Bodens und eine Optimierung der Kronenpflege implementiert werden, um die Resilienz der Wälder zu stärken.

Schlüsselwörter: Laubwälder, Rückgang der Krautschicht, Verschiebung der Artenzusammensetzung, naturnahe Bewirtschaftung, Langzeitüberwachung, Trockenstress

1 Introduction

“Closer-to-Nature” forestry, highlighted in the EU Forest Strategy for 2030, seeks to enhance both conservation value and climate resilience of managed forests in Europe by mimicking natural processes. This approach supports biodiversity and ecosystem resilience through methods like promoting structural diversity, encouraging natural regeneration, and maintaining continuous forest cover. Key principles include retaining habitat trees, preserving special habitats and dead wood, and promoting both native and site-adapted species (Bauhus et al. 2013, Larsen et al. 2022, Krumm et al. 2023).

The Steigerwald region, managed by the Ebrach State Forest Enterprise (BaySF), has implemented the concept of close-to-nature forestry for over five decades. Covering about 17,000 hectares, the management involves single-tree harvesting, fostering natural regeneration, and developing uneven-aged stands to balance biodiversity conservation with timber production (BaySF 2017, Mergner 2018, Mergner & Kraus 2020). Recognized as a key beech forest area in Germany, the Steigerwald also features significant oak and oak-hornbeam forests (Welss 1985, Müller et al. 2008, Sperber 2014).

Our study in the Steigerwald uses a resurvey approach to explore long-term changes (several decades) in layer structure and species composition. Layer structure refers to the vertical organization of vegetation, including tree, shrub, and herb layers, with a focus on forest floor vegetation such as herbaceous plants, mosses, and seedlings, which are essential for biodiversity and ecosystem function (Depauw et al. 2020). Changes in temperature, precipitation, soil moisture, nitrogen input, light availability, and management practices generally are key drivers of floristic changes (Reinecke et al. 2014, Bernhardt-Römermann et al. 2015, Fischer A., Fischer H.S. et al. (2015), Fischer A., Michler B. et al. (2015), Heinrichs & Schmidt 2017, Helm et al. 2017, Senf et al. 2020). To understand these changes, we analyse species traits, climatic data, and potential natural vegetation (PNV) models based on site-specific factors (Fischer et al. 2019).

Phytosociological relevés, which record species composition at specific sites, are crucial for tracking floristic changes over time. Repeated surveys at the same sites are commonly used to study long-term shifts in biodiversity and species composition (Röder et al. 1996, Naaf & Wulf 2010, Fischer et al. 2012, Bernhardt-Römermann et al. 2015, Fischer A., Fischer H.S. et al. (2015), Fischer A., Michler B. et al. (2015), Schmidt & Heinrichs 2015, 2017, Naaf & Kolk 2016, Hédl et al. 2017, Günther et al. 2021, Jandt et al. 2022).

In this study, we analysed 151 relevés from beech, oak, and oak-hornbeam forests in the Steigerwald, initially recorded in the years 1980 to 1982 (Welss 1985) and resurveyed in 2016 by the same author. Accurate marking of the original relevé positions allowed for precise relocation of semi-permanent plots. Our analysis examines changes over three decades in layer structure, species dynamics, and the main drivers of floristic changes, addressing the following questions:

Layer Structure: How has vegetation layer coverage changed?

Species Dynamics: Did species richness and evenness change? How did individual species’ cover and frequency shift? Did species composition in the overstory and understory alter? What influence have management practices had, especially on forest floor vegetation?

Environmental Factors: Which environmental factors explain the observed changes in forest floor plant species composition?

By examining layer structure and forest floor vegetation, our study aims to shed light on the effects of close-to-nature forest management on biodiversity and resilience in forest ecosystems.

2 Study area

The plots are set in a state forest area in the “Steigerwald”, a low mountain range (up to 498 meters above sea level) in southern Germany (Federal State of Bavaria, N 49°50′; E 10°29′). A variety of rock types from the Lower and Middle Keuper form a small-scale mosaic of marly, clayey, and sandy soils.

The historical management of the Steigerwald forest has evolved significantly over the past centuries, influenced by political, social, and economic factors. Initially managed by local nobility and ecclesiastical authorities, the forests were primarily used for timber production and agriculture. In the 17th and 18th centuries, coppice-with-standards was a common practice, promoting species like oak and hornbeam. During the 19th century, management shifted towards high forests dominated by beech, using shelterwood cutting techniques. In the 20th century, a shift towards close-to-nature forestry began, emphasizing both single-tree harvesting and natural regeneration, respectively, to preserve the beech-dominated character of the forest. Today, the Steigerwald employs an integrative approach that balances timber production with biodiversity conservation, aiming to create resilient and adaptive forest ecosystems (Mergner & Kraus 2020).

According to BaySF (2017) and Mergner & Kraus (2020), the recent forest stands are composed mainly of broadleaved (73%) species. Beech (*Fagus sylvatica*) is the dominant tree species (40%), followed by Oak (mainly *Quercus petraea,* 21%). Conifers account for 27%. Scots Pine (*Pinus sylvestris,* 15%) is the most frequent conifer species followed by Norway Spruce (*Picea abies,* 7%) and larch (*Larix decidua,* 4%). The actual timber stock is 388m^3/ha, the annual growth amount to 10.8m^3/ha/a. 70% of the annual growth is harvested. In total, 12% of the forest area is set aside.

A great majority of the forests in the study area represents ancient forests, i.e. they are managed as forests since more than 200 years (Glaser & Hauke 2004, Sperber 2014).

The predominant forest types, as described by Welss (1985), Fischer (2003), Fischer et al. (2019) and Walentowski et al. (2020) include the following:

- Luzulo-Fagetum, beech forests (Luzulo-Fagetum Meusel 1937); EU-habitat type 9110, beech forests on acidic soils,
- Galio odorati-Fagetum, beech forests (Galio odorati-Fagetum Sougnez et Thill 1959 nom. conserv. propos.); EU-habitat type 9130, beech forests on soils with intermediate pH,
- Luzulo-Quercetum, oak forests (Luzulo-Quercetum petraeae Hilitzer 1932 nom. invers. propos.); no EU-habitat type, oak forests on very dry soils,
- Galio-Carpinetum, oak-hornbeam forests (Galio-Carpinetum Oberdorfer 1957); EU-habitat type 9170, oak-hornbeam forests.

The nomenclature of the forest communities follows Rennwald (2000).

3 Methods

3.1 Field survey

From 1980 to 1982, Walter Welß studied the forest vegetation of the Steigerwald by recording more than 500 phytosociological relevés. He documented the position of the relevés by exact descriptions of each locality and with marks in a map 1:10,000. The goal at that time was to get a representative picture of the forest vegetation of the study area, thus he selected the plots in the area as evenly distributed as possible (Welss 1985). In 2016, plots representing beech, oak, and oak-hornbeam forests, located within the state forest managed by the Ebrach State Forest Enterprise (BaySF), were selected. Walter Welß himself resurveyed 151 of these relevés, guaranteeing the maximum degree of continuity in data sampling as possible. The size of the relevés varied between 300 and 400m^2. He recorded all vascular plants and cryptogams growing on the ground. Nomenclature of the species follows GermanSL 1.4 (Jansen & Dengler 2008). In 1985, Welß recorded cover-abundance-values with a seven-level cover-abundance scale according to Braun-Blanquet (1964). In 2016, he estimated cover values directly.

In the field we distinguished five vegetation layers: tree layer (T): woody plants (height > 5m); shrub layer (S): woody plants (height > 1m and < 5m); herb layer (H): all vascular plants (including regeneration of woody plants (height < 1m), moss layer (M): cryptogams growing on the soil. In vertical stratified stands, we divided the tree layer in an upper tree layer (tree layer 1) and a lower one (tree layer 2). The two tree layers form the overstory. Shrubs plus herb layer and moss layer form the understory.

In 2016, the number of stumps and their decay stage were used to describe the management history of the plots. The decay stage of each stump was assessed on a five-level scale following (Keller 2005): recently dead, weakly decayed, moderately decayed, very decayed, and almost decomposed.

3.2 Data analysis

All analyses were conducted using the statistical programming language R version 4.2.2 (R Core Team 2021; RStudio Team 2021), employing the packages dave (Wildi 2017), dplyr (Wickham, François et al. 2023), ggplot2 (Wickham, Chang et al. 2023), vegan (Oksanen et al. 2022), and multcompView (Graves et al. 2023).

To enable quantitative comparisons between the two survey years, Braun-Blanquet cover values from 1985 were converted to their corresponding midpoint percentage values, following the recommendation of Ellenberg et al. (2001). In contrast, continuous percentage estimates from 2016 were used directly for analysis.

To assess the potential influence of differing measurement approaches, the 2016 data were also transformed into Braun-Blanquet cover classes, allowing for categorical comparison with the 1985 dataset. Due to the right-skewed nature of the Braun-Blanquet scale – where low cover values dominate – the midpoint transformation may slightly overestimate 1985 values. However, this methodological effect is minimal. A detailed evaluation of cover class transitions is presented in Appendix 1.

3.3 Detecting changes in layer structure

3.3.1 Building layers, calculating layer cover and layer cover changes

We reorganized the five layers recorded in the field and introduced three additional layers to better assess the natural regeneration of tree species. Specifically, to evaluate the regeneration in the shrub layer, we separated the cover values of naturally regenerating trees from those of other woody plants. This process resulted in the following layers: “natural regeneration of tree species in the shrub layer” and “other shrubs.” Similarly, within the herb layer, we distinguished the cover of natural regeneration from that of herbs and mosses, leading to the layers: “natural regeneration of tree species in the herb layer” and “herb layer (including mosses) without natural regeneration of tree species.”

Ultimately, we analysed the following six layers:

- Tree layer 1: Represents the primary tree canopy
- Tree layer 2: Represents the secondary tree canopy
- Natural regeneration in the shrub layer: Indicates young trees regenerating in the shrub layer
- Other shrubs: Includes shrubs other than regenerating trees
- Natural regeneration in the herb layer: Indicates young trees regenerating in the herb layer
- Herb layer without natural regeneration: Includes herbs and other ground vegetation, excluding tree regeneration

3.3.2 Calculating and analysing layer cover

For each relevé, we calculated the cover of the six vegetation layers based on the cover values of the species present, following the method described by Fischer (2015). The cover of a particular layer in a relevé is determined by summing the cover values of all species constituting that layer, while accounting for assumed random overlaps. We consider this approach, which is based on detailed estimates of individual species coverage, to be more precise than an overall estimate of layer coverage across 400 m².

We analysed whether the total cover of these layers differed between years using a paired Wilcoxon test ($p < 0.05$). Additionally, we combined tree layer 1, tree layer 2, and the shrub layers into a single “woody layer” to assess the shading effect of woody plants on the herb layer. Using regression analyses, we studied the influence of the woody layer and the effect of the year on the herb layer.

3.4 Assessing species dynamics

3.4.1 Species richness, species evenness

Species richness (number of species) and evenness for each relevé were calculated for the herb layer and we analysed whether they differ between record years (paired Wilcoxon-test, $p < 0.05$). Moreover, we determined change of richness and evenness between years for each relevé to intend the proportion of change between years.

3.4.2 Determining changes in abundance of single species

We tested whether single species in the overstory and understory increased or decreased significantly between record years using a paired Wilcoxon test ($p < 0.05$).

3.4.3 Determining changes in the species composition of overstory and understory

We merged the surveys from 1985 and 2016 into one dataset and analysed the species composition of the overstory and understory separately because tree layer composition largely depends on forest management, whereas the understory reflects the natural growing conditions of forest types.

We analysed the overall change in species composition of the overstory and understory using correspondence analyses (CA) without down-weighting rare species to visualize overall changes of plots between years. Significance was tested using an analysis of similarities (ANOSIM) with the “anosim” function from the vegan package (Oksanen et al. 2022) with Jaccard’s similarity index and 10,000 iterations.

The classification of the overstory reflects preferred tree species composition shaped by forest management, while the classification of the understory identifies forest types. We applied Ward’s method with the Jaccard similarity index for samples and chord distance for species to classify the species. Characteristic species for each forest type were identified using analysis of variance (ANOVA).

We conducted correspondence analyses of species and relevé groups ordering the groups in the vegetation table according to this CA to illustrate the main trends in tree species mixtures in the overstory and key environmental gradients in the understory.

By calculating the mean cover of the dominant tree species (those with the highest cover values in the overstory: beech, oak, hornbeam, spruce, and Scots pine), we determined the tree species composition for each forest type in the understory. Additionally, we assessed the cover of Tree Layer 1, Tree Layer 2, natural regeneration in the shrub layer, other shrubs, natural regeneration in the herb layer, and the herb layer without natural regeneration within the understory forest types, along with species richness and evenness, to characterize their diversity. This comprehensive approach provides a detailed understanding of species composition, layering, and diversity across the forest types.

Changes in species composition can lead to shifts in forest type membership over time. If species composition within the plots remains stable between surveys, the relevés consistently cluster within the same forest type. However, significant compositional changes can cause plots to shift their forest type affiliation from one survey to the next. These shifts were visualized using a confusion matrix and Sankey diagrams (generated with the geom_alluvium function from the *ggplot2* package, (Wickham et al. 2023)). The diagrams highlight the transitions in forest type affiliation of the relevés between 1985 and 2016, illustrating how changes in species composition and cover influenced the clustering of relevés within or across units over time.

Color-coding (Appendix 3) helps differentiate the years, while the confusion matrix provides a more detailed analysis of vegetation dynamics (Tab. 1). The matrix compares the assignment of relevés (vegetation plots) to forest types within the understory in 1985 and 2016. Rows correspond to forest type membership in 1985, while columns represent membership in 2016. The diagonal fields indicate "constant relevés", or those that remained within the same forest type. In contrast, "changing relevés" are those that shifted to another unit, while "newcomers" refer to relevés that newly joined the unit.

In addition, we conducted a detailed analysis of species composition changes in the understory. For each forest type, we separated plots with constant and changing forest type affiliation. We then identified species that significantly differed between the years within the constant and changing relevés using ANOVA ($p < 0.05$).

Furthermore, we analysed whether the cover of the layers changed significantly in constant and changing plots using the Wilcoxon test ($p < 0.05$).

3.4.4 Impact of management on vegetation dynamics

To assess the impact of management practices on vegetation dynamics, we used the number and decay stage of tree stumps as indicators of past interventions such as logging or thinning. A matrix was constructed with decay stages as rows, plots as columns, and stump counts as cell values. After column-wise normalization, the matrix was subjected to classification, resulting in four plot groups with similar stump composition and decay profiles.

We then tested whether the cover of individual species differed significantly between the management groups using the Kruskal-Wallis test ($p < 0.05$). In addition, we analysed whether changes in species richness and evenness between 1985 and 2016 differed significantly among these groups, also using the Kruskal-Wallis test ($p < 0.05$).

To assess changes in vegetation structure, we calculated cover differences (2016 minus 1985) for the upper and lower tree layers, the shrub layer, natural regeneration of tree species in the herb layer, and the herb layer excluding tree regeneration. These changes were likewise tested for significant differences between the four management groups using the Kruskal-Wallis test ($p < 0.05$).

Finally, to investigate the influence of logging infrastructure, we compared the change in herb layer cover between plots with ($n \approx 1/3$) and without ($n \approx 2/3$) skid trails (Rückegassen). Statistical differences between the two groups were assessed using both a Welch two-sample t-test and a Wilcoxon rank-sum test ($p < 0.05$).

3.5 Finding main drivers to interpret floristic changes in the herb layer

We derive information from three sources: (i) the vegetation itself, (ii) data from the weather station, and (iii) the potential natural vegetation (PNV), which is the result of modelling based on site factors. We analysed Ellenberg indicator values and Raunkiaer life forms (Ellenberg et al. 2001) of the herb layer (excluding tree seedlings) and used climatic data from the German Meteorological Service (Deutscher Wetterdienst, www.dwd.de), sourced from the weather station in Ebrach, which is centrally located in the study area. Although direct measurements of the microclimate were not available, it is known that macroclimate and microclimate are correlated in forests (Zellweger et al. 2020). Therefore, we used macroclimatic data as an approximation. The concept of Potential Natural Vegetation (PNV) is widely used to characterize complex site conditions through specific forest types. We analysed scenarios of current and future PNV for both the region and the plots. The distribution of PNV forest types in the scenarios is derived from models based on soil and climatic maps, as well as distribution maps of forest types (Fischer et al. 2019).

3.5.1 Ellenberg indicator values and Raunkiaer life forms

Due to the lack of direct measurements of site factors, we calculated the mean values of Ellenberg indicator values for each relevé in every year to provide basic information on environmental conditions. To do this, we used weighted arithmetic means, with square root-transformed cover values as weights. This weighting method aligns with the approach proposed by Ellenberg (1979, p. 21), which accounts for the fact that species tend to have higher cover values when they are close to their ecological optimum. We then analysed whether these weighted arithmetic means differed between record years using the Wilcoxon test ($p < 0.05$).

However, reducing indicator values to a single mean can oversimplify the data. More detailed insights can be obtained from the spectra of indicator values. Additionally, since indicator values are, strictly speaking, ordinal scales, they should not be averaged. For these reasons, we also calculated the spectra of indicator values. For each year (1985 and 2016) and each indicator (light, temperature, continentality, moisture, soil acidity, nitrogen availability), we performed the following steps:

- Summing cover values: We summed up the cover values of all species that fell into each category of the indicator. For example, for the light indicator, we would sum the cover values of species in categories like "category 1: full shadow plant", "category 3: shadow plant", "category 5: half shadow plant", "category 7: half-light plant", "category 9: full-light plant".
- Averaging by number of relevés: We then divided this sum by the total number of relevés ($n = 151$). This gave us the average cover value for each category of the indicator.
- Resulting spectra: This process provided us with a spectrum of categories based on the mean cover values for each indicator in both 1985 and 2016. In other words, we could see the average cover values for each category (e.g., light levels) for both years.
- Raunkiaer Life Forms: Similarly, we calculated the annual mean cover values for Raunkiaer life forms (different plant growth forms) following the same method, based on Ellenberg et al. (2001).

This approach allowed us to compare how the mean cover values for various ecological indicators and plant life forms changed over the 31-year period.

3.5.2 Climatic data

Basis for calculation climatic data are the daily mean, minimum and maximum of air temperature 2m above ground from the years 1963 to 2019, using data from the climate station Ebrach (located in the Steigerwald) of the German Weather Broadcast Service (Deutscher Wetterdienst, DWD). We determined the number of ice days (maximum temperature below 0 °C), frost days (minimum temperature below 0 °C), summer days (maximum temperature above 25 °C) and very hot days (maximum temperature above 30 °C) per year. We also calculated a linear regression from mean daily temperature to years (1963 to 2019).

3.5.3 PNV

Fischer et al. (2019) developed a model for the entire Bavaria region with a resolution of 50 meters to predict distribution maps of potential natural vegetation (PNV) units based on soil and climatic data under current and future conditions. We applied these maps to determine the current and future (+1K) PNV-unit for each plot and the entire region.

4 Results

4.1 Layer structure

The cover of the upper tree layer decreased slightly, while the cover of the lower tree layer increased marginally (Fig. 1). The natural regeneration of tree species in the shrub layer showed a moderate increase. In the herb layer, we observed a low cover of natural regeneration for tree and shrub species, with no significant difference in the mean. The presence of other shrubs in the shrub layer remained low. In contrast, the cover of herbs and mosses in the herb layer declined sharply, dropping from a median of 55% to 16% per site (Fig. 1, Fig. 2).

The components of the understory exhibited different trends: while shrubs slightly increased, the natural regeneration of trees in the herb layer showed no significant change, and the herb layer experienced a dramatic decrease.

The cover of the woody layer (trees and shrubs) increased only slightly. This woody layer casts shade on the herb layer (Fig. 2). In 1985, the herb layer cover was weakly dependent on the woody layer cover ($p = 0.04$), with a very low R^2 value of only 2% (linear regression). By 2016, this relationship was no longer significant. However, the influence of the year itself was stronger, with an adjusted R^2 of 24%.

The cover of natural regeneration in the shrub layer did not significantly affect the herb layer cover in either year.

Although shading plays a significant role, the low R^2 value indicates that it is relatively minor compared to the effect of the year. Therefore, the substantial differences in herb layer cover observed between the beginning and end of the observation period cannot be explained solely by shading by woody plants.

4.2 Species dynamics

4.2.1 Herb layer: species richness and evenness

We found 194 species in the herb layer across the 302 plots (2 x 151 plots). The boxplots (Fig. 3, left) show that both species richness and species evenness in 1985 and 2016 had p-values greater than 0.05, indicating no significant differences between the two years. The histograms (Fig. 3, right) on the right depict the change in species richness and species evenness per plot, with the dashed line representing the median of these changes. The distribution of changes is centred around zero, suggesting no change in species richness and evenness over the period.

4.2.2 Change in abundance of single species

In the overstory, only one species showed a significant change between years: *Sorbus torminalis* (Wild service tree) increased, a species known for its preference for warm conditions. In contrast, in the understory vegetation, 76 out of 272 species (27%) exhibited significant changes in cover: 21 species increased, while 55 decreased. Appendix 2 provides a list of species with significant changes in cover.

Several species demonstrated substantial increases in cover and frequency over the study period. For example, *Fagus sylvatica* as part of the shrub layer showed a significant increase in cover from 0.8 in 1985 to 12 in 2016, with frequency rising from 12 to 108 plots. This increase suggests a robust regeneration of beech trees, possibly driven by the forest management practices favouring natural regeneration. Similarly, *Rubus fruticosus* agg. (Blackberry) in the herb layer saw its cover rise from 0 to 1, and its frequency jumped from 0 to 47 plots, indicating that blackberry is associated with increased light and nutrient availability and disturbance, has become more prevalent. *Impatiens parviflora* (neophyte) also increased in cover from 0 to 0.7 and appeared in 33 plots in 2016, up from none in 1985. This species is known for its rapid colonization ability, particularly in disturbed or slightly modified habitats. Similarly, other species like *Acer platanoides* (Norway Maple) and *Acer pseudoplatanus* (Sycamore Maple) in the shrub layer showed notable increases in cover and frequency, reflecting shifts in the shrub layer dynamics, possibly influenced by canopy gaps and altered light conditions. Additionally, *Urtica dioica* increased in cover from 0.02 to 0.09 and in frequency from 6 to 24 plots, which may be associated with nutrient enrichment or increased light levels in the understory. *Galium aparine,* another species favouring nutrient-rich conditions, increased in cover from 0 to 0.09 and appeared in 11 plots in 2016, highlighting shifts in the herb layer composition toward species that thrive in disturbed or enriched conditions.

Conversely, numerous species experienced significant declines in both cover and frequency, highlighting a shift away from certain understory components. For instance, *Luzula luzuloides* showed a drastic reduction in cover from 7 in 1985 to 1 in 2016, with its frequency declining from 96 to 83 plots. *Galium odoratum,* which is commonly found in beech forests, also declined significantly in cover from 7 to 2, although its frequency remained constant across 80 plots.

Milium effusum, a shade-tolerant species, decreased in cover from 3 to 2, and its frequency dropped from 68 to 65 plots. Similarly, *Oxalis acetosella,* known for thriving in moist, shaded forest floors, declined from 1 to 0.1 in cover, with a corresponding drop in frequency from 44 to 29 plots. *Deschampsia flexuosa* experienced one of the most significant declines, with cover falling from 4 to 1 and frequency decreasing from 65 to 40 plots.

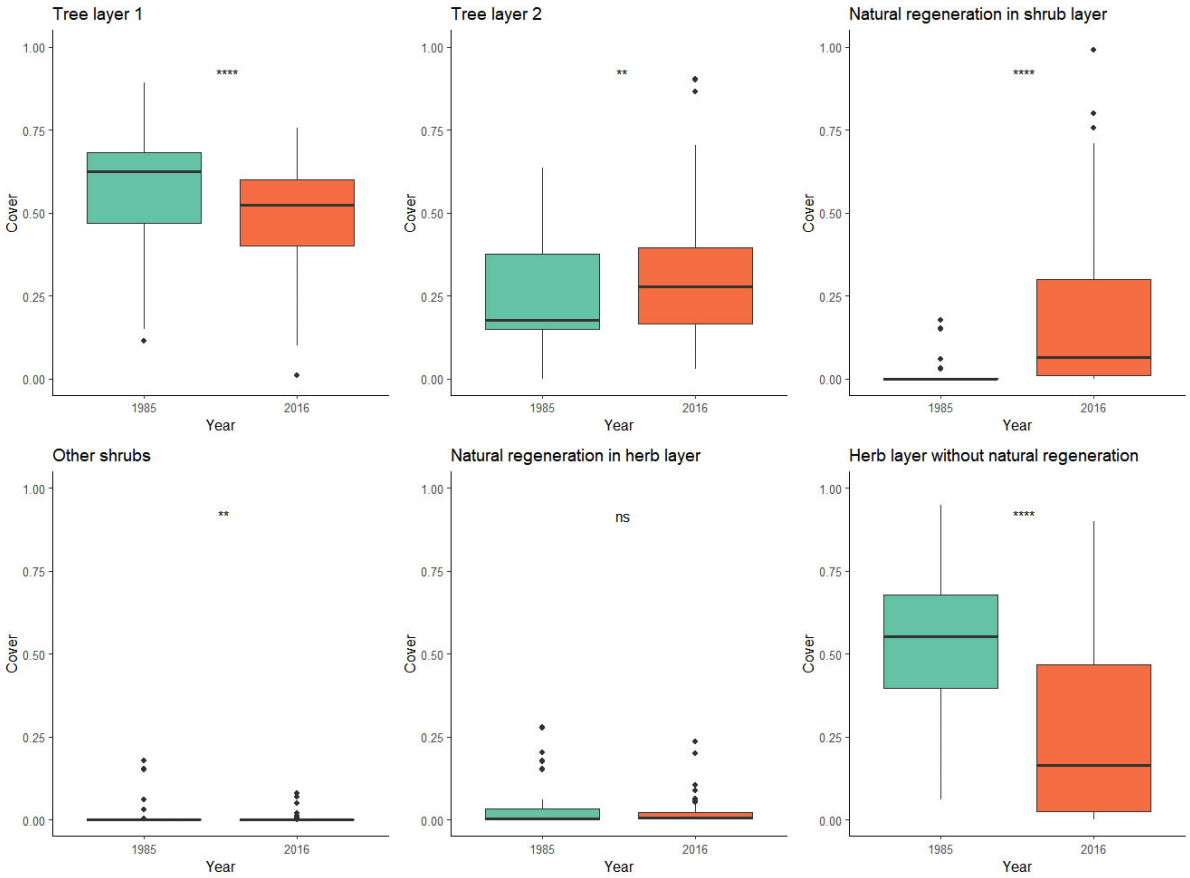

Fig. 1: Cover differences of tree, shrub and herb layer between 1985 and 2016. **: p < 0.01; ***: p < 0.001; n.s: p > 0.05.

Abb. 1: *Änderung der Deckung der Baum-, Strauch- und Krautschicht von 1985 bis 2016.*

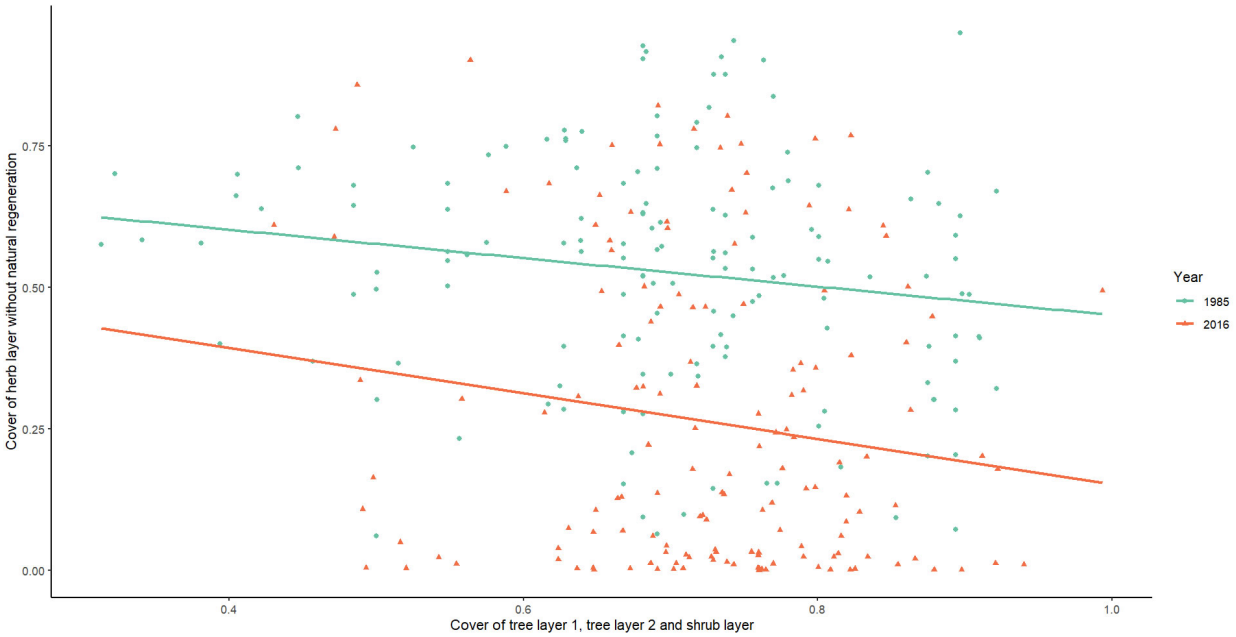

Fig. 2: Relation (bivariate regression) between cover of herb layer and cover of woody layer (combination of tree layer 1, tree layer 2 and shrub layer) and year of observation. Woody layer: 1985: R^2-squared: 0.02, p-value: 0.04; 2016: R^2: 0.017, p = 0.057; Year: R^2: 0.24; p < 2.2e-16.

Abb. 2: *Beziehung (bivariate Regression) zwischen der Deckung der Krautschicht und der Deckung der Gehölze (Baumschicht 1 und 2 sowie Strauchschicht) und dem Jahr der Erhebung.*

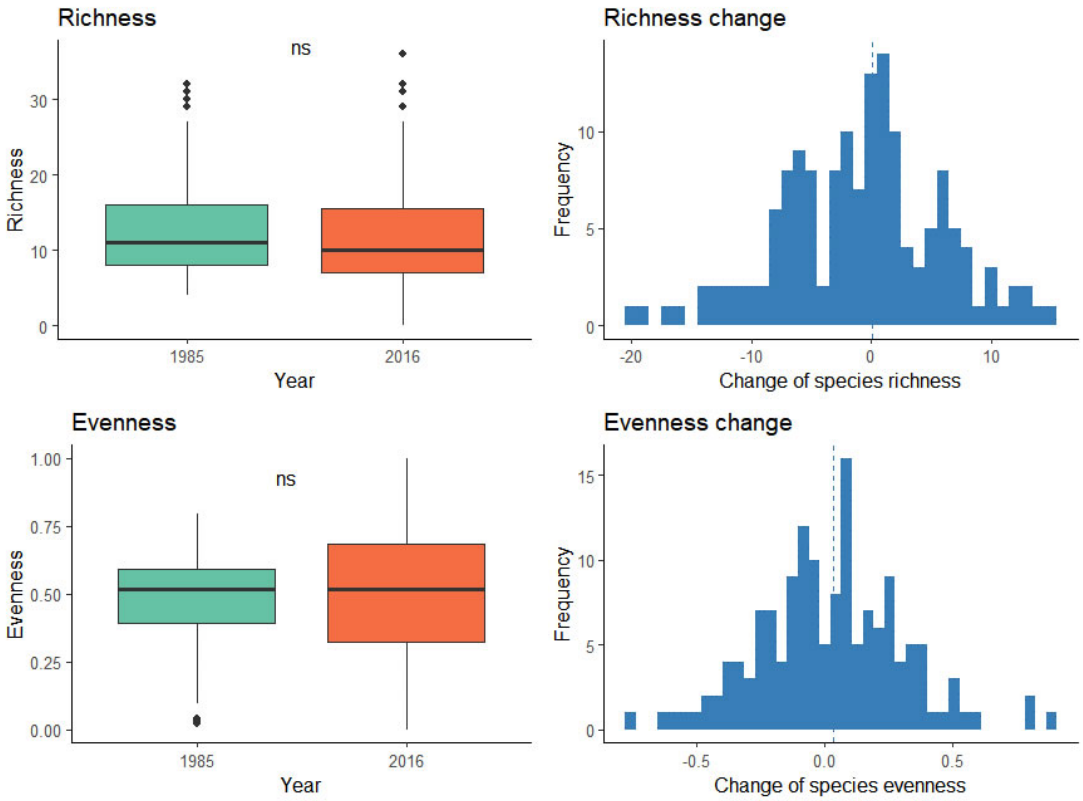

Fig. 3: Boxplots (left) and histograms (right) illustrating changes in species richness (top) and species evenness (bottom) in the herb layer between the years 1985 and 2016. p-values > 0.05, dashed line: median.

Abb. 3: *Links: Artenreichtum und Evenness 1985 und 2016 in der Krautschicht, p-Wert > 0.05; rechts: Veränderung des Artenreichtums und der Evenness pro Aufnahmefläche, gestrichelte Linie: Median.*

Overall, the findings suggest that in the understory natural regeneration of tree layer species, generalists and nutrient indicators has increased moderately, while herbs typically for beech forests have declined.

4.2.3 Overall change of species composition between years

Correspondence analysis of the overstory in 1985 (green) and 2016 (red) together (Fig. 4, right) showed minor changes in species composition of the overstory (ANOSIM, $p < 0.03$). The large ellipses encompass 90% of the relevés from 1985 and 2016, respectively, and both ellipses are almost the same size. In contrast, the correspondence analysis of the understory reveals that the variability (degree of dissimilarity) significantly decreased from the older (larger, green ellipse) to the more recent relevés (narrower, red ellipse) (Fig. 4, left). This indicates that the species composition of the understory vegetation has become more homogeneous over the last three decades (ANOSIM, $p < 0.0001$).

4.2.4 Overstory species composition

The classification of tree layer species is illustrated in Fig. 5, which displays the tree species mixtures present in the plots, distinguishing 13 groups. The columns in the table are color-coded according to the year the samples were recorded, with all groups consisting of relevés from both 1985 and 2016.

Beech (*Fagus sylvatica*) is present in nearly all relevés, except in group 1, in samples recorded in both 1985 and 2016. The left branch (groups 5, 12, 3, 7, 10, 1) contains stands with beech, partially mixed with sessile oak (*Quercus petraea*) and hornbeam (*Carpinus betulus*). In the right branch (groups 13, 2, 11, 9, 8, 4, 6), beech is the dominant tree species, partially mixed with sessile oak and conifers (*Pinus sylvestris, Picea abies, Larix decidua*), with no hornbeam present. Groups 13, 2, and 11 are characterized by beech and oak, while groups 9, 8, and 4 have a higher proportion of coniferous trees. The forests in the far-right group (6) are composed mainly of beech.

4.2.5 Change of overstory species composition

The Sankey diagram (Fig. 6) illustrates the changes in forest type membership of tree species between 1985 and 2016. Each group on the left represents the tree layer classification in 1985, while the groups on the right represent the classification in 2016. The flows between the two sides indicate the transitions of plots from one group to another over the 30-year period. The thickness of the flows represents the number of plots transitioning from one group to another. Thicker flows indicate a higher number of plots undergoing similar transitions. Out of 151 plots, 81 (53%) did not change their group affiliation, as shown by the flows that remain within the same group from 1985 to 2016. This suggests a high level of stability in species composition for over half of the plots. While most groups have remained stable, there are minor transitions where some plots have moved from one group to another. These transitions could indicate slight changes in the species composition, possibly due to forest management practices. Groups 9, 8, and 4, which represent plots with admixtures of coniferous trees, have shown a noticeable

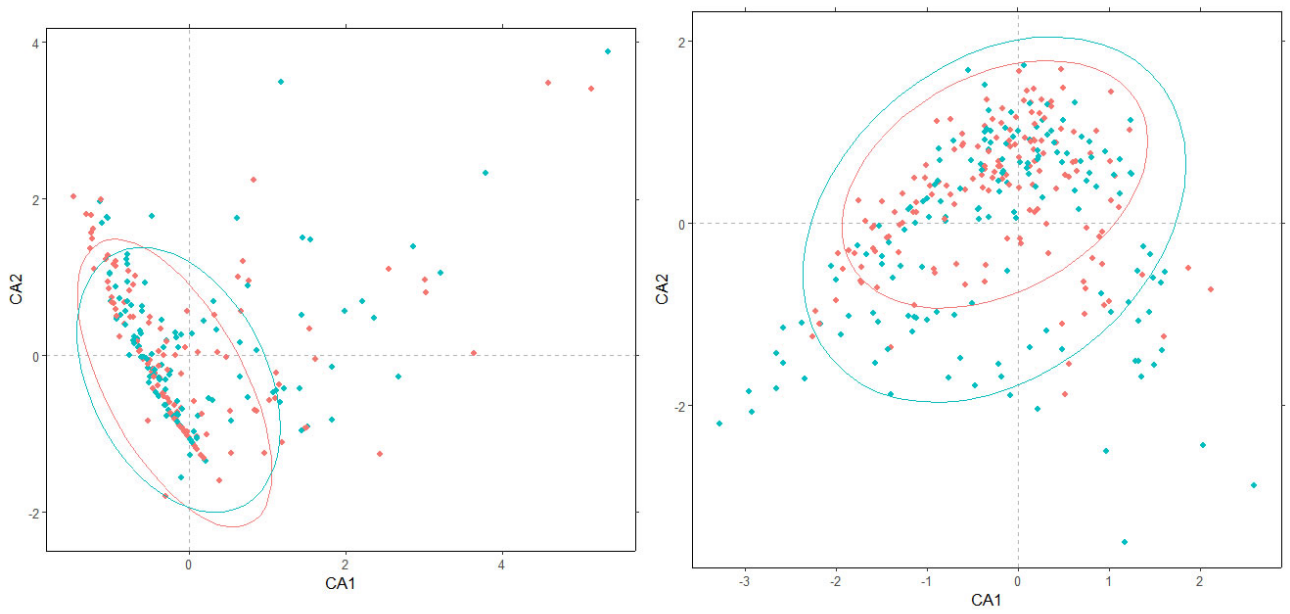

Fig. 4: Correspondence analysis of relevés from 1985 (green) and 2016 (red). Left overstory, right understory. Ellipses indicate the central area encompassing 90% of the relevés.

Abb. 4: *Korrespondenzanalyse der Aufnahmen von 1985 (grün) und 2016 (rot). Links: Baumschicht, rechts: Unterwuchs. Die Ellipsen zeigen den zentralen Bereich, der 90 % der Vegetationsaufnahmen umfasst.*

decrease in size from 1985 to 2016. This suggests a potential decline in the presence of coniferous trees within these groups, possibly due to changes in management practices that eliminate non-site-appropriate conifers.

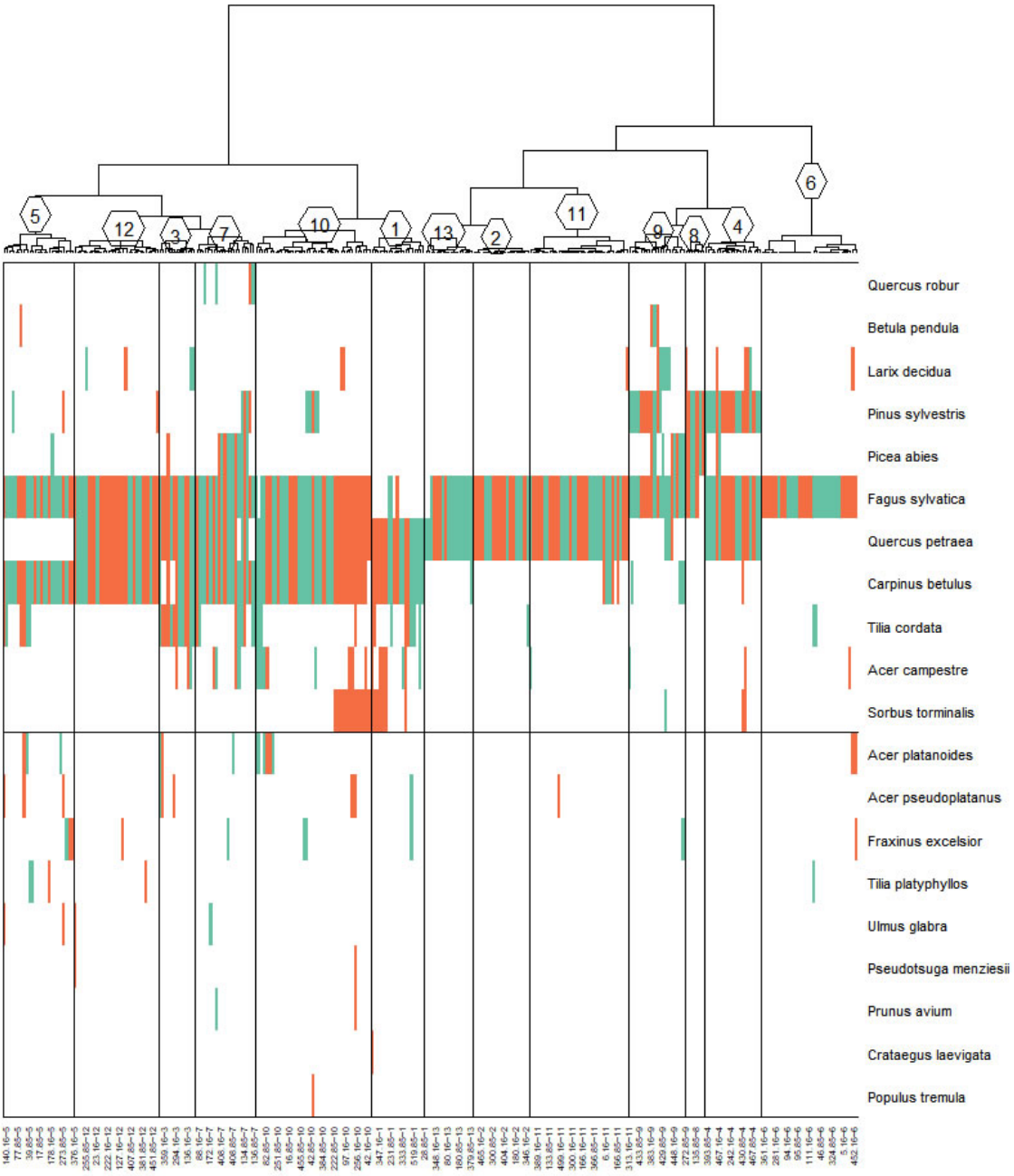

Fig. 5: Classification of species composition of tree layer (151 relevés from 1985, green and 151 relevés from 2016, red).

Abb. 5: *Artzusammensetzung der Baumschicht (151 Aufnahmen von 1985, grün und 151 Aufnahmen von 2016, rot).*

4.2.6 Understory species composition

The classification of understory vegetation identified 13 distinct forest types, each with a unique species composition. Figure 7 presents the classification as a dendrogram. The left branch of the dendrogram includes forest types found on acidic soils, *Quercion roboris* Malcuit 1929 (forest type 2) and *Luzulo-Fagion* Lohmeyer et Tx. in Tx. 1954 (forest types 6, 4, 7). The central branch of the dendrogram represent beech forests on base-rich soils, *Fagion sylvaticae* Luquet 1926 (forest types 8, 10, 3, 11, 12, 5, 13, and 9). The right branch (forest type 1) corresponds to oak-hornbeam forests (*Carpinion betuli Issler 1931*). The vegetation table in Appendix 3 lists all species that significantly differentiate between units.

Figure 8 illustrates the tree species composition and their proportion within the units (mean cover values in the relevés). Beech, oak, and hornbeam are common across most forest types, while the admixture of coniferous trees is minimal.

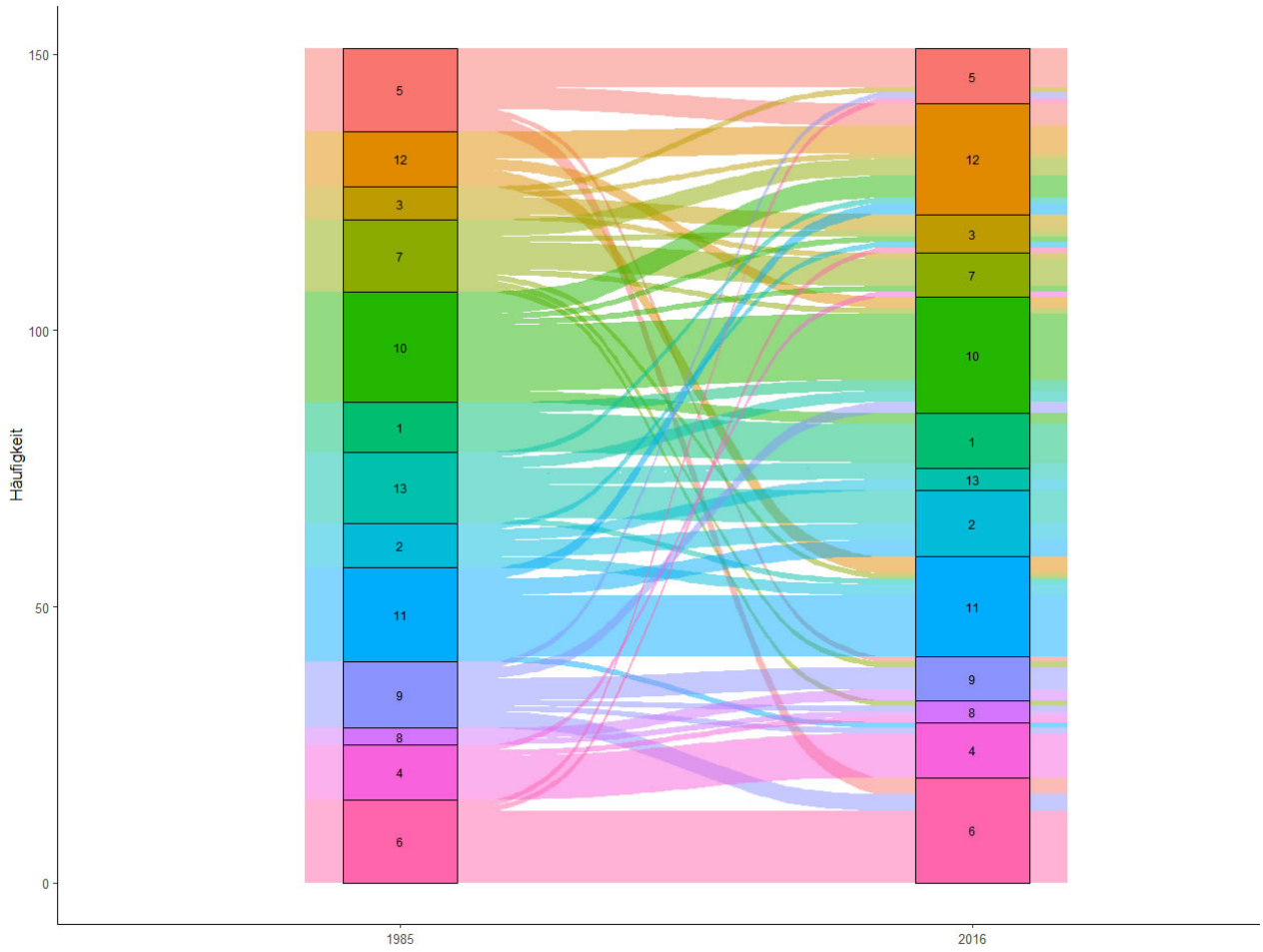

Fig. 6: Sankey diagram showing changes in group affiliation within the tree layer; left: group affiliation in 1986, right: group affiliation in 2016; bands indicate the changes in affiliation; the order of groups from top (group 5) to bottom (group 6) follows the order in the dendrogram (Fig. 5) from left to right.

Abb. 6: *Sankey-Diagramm zur Darstellung der Veränderung der Gruppenzugehörigkeit in der Baumschicht; links: Gruppenzugehörigkeit 1986, rechts: Gruppenzugehörigkeit 2016; die Bänder zeigen die Veränderungen der Zugehörigkeit an; die Reihenfolge der Gruppen von oben (Gruppe 5) nach unten (Gruppe 6) folgt der Reihenfolge im Dendrogramm (Abb. 5.) von links nach rechts.*

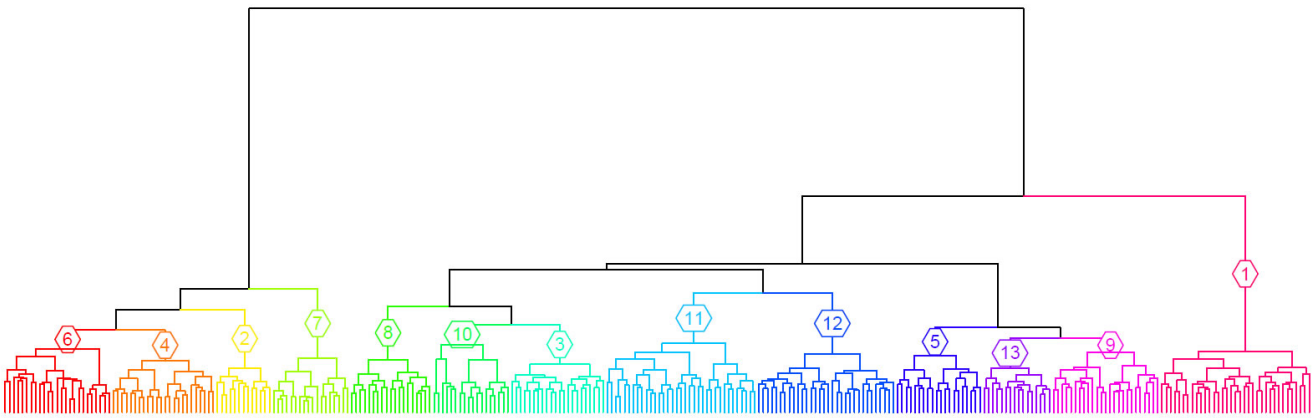

Fig. 7: Classification (dendrogram) of species of understory vegetation (relevés from 1985 and 2016) resulting in 13 forest types: Forest types 6, 4, 7: beech forests on base poor soils (*Luzulo-Fagion* Lohmeyer et Tx. in Tx. 1954), Forest type 2: oak forests (*Quercion roboris* Malcuit 1929), Forest types 8, 10, 3, 11, 12, 5, 13, 9: beech forests on base rich soils (*Fagion sylvaticae* Luquet 1926), Forest type 1: oak-hornbeam forests (*Carpinion betuli* Issler 1931).

Abb. 7: *Klassifikation (Dendrogramm) des Unterwuchses (Aufnahmen von 1985 und 2016) ergab 13 Vegetationseinheiten:* Vegetations*einheiten 6, 4, 7: Buchenwälder auf basenarmen Böden:* (Luzulo-Fagion), *Vegetationseinheit 2: Eichenwälder* (Quercion roboris), *Vegetationseinheiten 8, 10, 3, 11, 12, 5, 13, 9: Buchenwälder auf basenreichen Böden* (Fagion sylvaticae), *Vegetationseinheit 1: Eichen-Hainbuchenwälder* (Carpinion betuli).

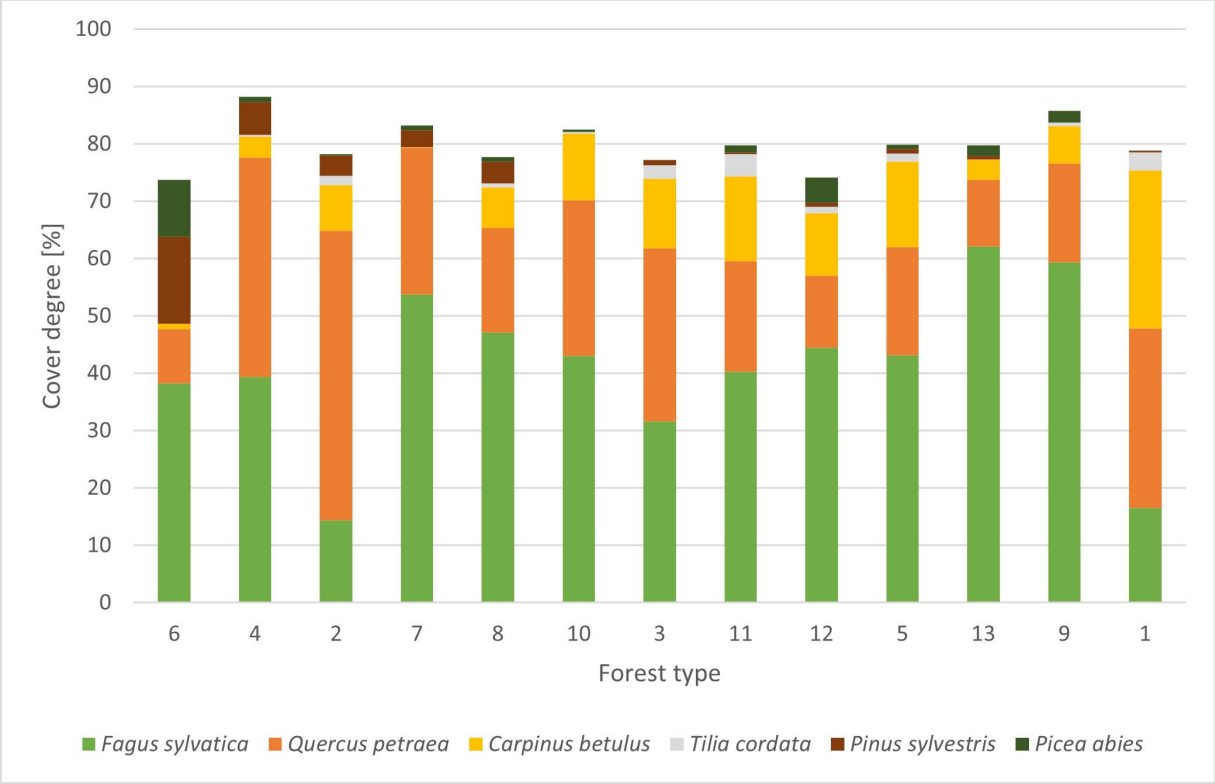

Fig. 8: Tree species composition of the forest types (legend see Figure 7).

Abb. 8: *Baumartenzusammensetzung der Vegetationseinheiten (Legende s. Abb. 7).*

Figure 9 provides boxplots showing the cover of six vegetation layers across the forest types. The boxplots reveal significant differences in the cover of certain layers, particularly Tree Layer 1 and the Herb Layer excluding natural regeneration. In contrast, the other layers exhibit more consistent cover across the forest types.

Species richness varies notably between the units (Fig. 10). Forest type 1 (oak-hornbeam forests) shows the highest median species richness (28 species), followed by Unit 3 (26) and 12 (24) (beech forests on base-rich soils). The lowest richness is found in Unit 7 (7 species) and Unit 9 (9 species). The other units fall in between, such as *Luzulo-Fagion* units 6, 4, and other beech forests on base-rich soils like Units 8, 10, 11, 5, and 13. Species evenness is similar across most units. However, Unit 8 (beech forests on base-rich soils) shows a more uneven distribution, with a few species dominating.

Beech and oak forest types on base-poor soils (forest types 6, 4, 2 and 7):

These forest types are characterized by species indicative for acidic soils, such as *Deschampsia flexuosa, Luzula luzuloides, Vaccinium myrtillus,* and *Polytrichum formosum*.

- Forest type 6 is dominated by beech (38%), accompanied by Scots pine (15%) and spruce (10%). This unit corresponds to the Luzulo-Fagetum.
- Forest type 4 features a mixture of beech (39%) and oak (38%) in the tree layer.
- Forest type 2 is primarily composed of oak (50%). This unit belongs to the *Quercion roboris* alliance.
- Forest type 7 is dominated by beech (54%) with oak (26%) as an admixture. Like Unit 4, it corresponds to the Luzulo-Fagetum but differs by having fewer coniferous species in the tree layer and a higher beech cover.

Beech forest types on base-rich soils (forest types 8, 10, 3, 11, 12, 5, 13, and 9):

In these units beech dominates the tree layer, with some admixture of oak, hornbeam, and minimal coniferous trees. These units belong to the *Fagion sylvaticae* alliance, they are characterized by species like *Poa nemoralis, Melica uniflora, Galium odoratum, Milium effusum* and *Dryopteris filix-mas*.

- Forest type 8 has beech (47%), oak (18%) and hornbeam (7%) in the tree layer. The herb layer include species indicating base poor soil conditions like *Luzula luzuloides* and *Polytrichum formosum*.
- Forest type 10 consists of beech (43%), oak (27%) and hornbeam (12%). The herb layer includes characteristic *Fagion sylvaticae* species and natural regeneration of oak and hornbeam.
- Forest type 3 is dominated by beech (32%), oak (30%) and hornbeam (12%). Natural regeneration of *Tilia cordata* (Small-leaved Lime) occurs in both the herb and shrub layers. The characteristic species of the *Fagion sylvaticae* emphasize in this unit, but also some species characteristic of *Quercion roboris* and *Carpinion betuli* alliances occur. The unit is species-rich with *Urtica dioica* indicating good nutrient availability.

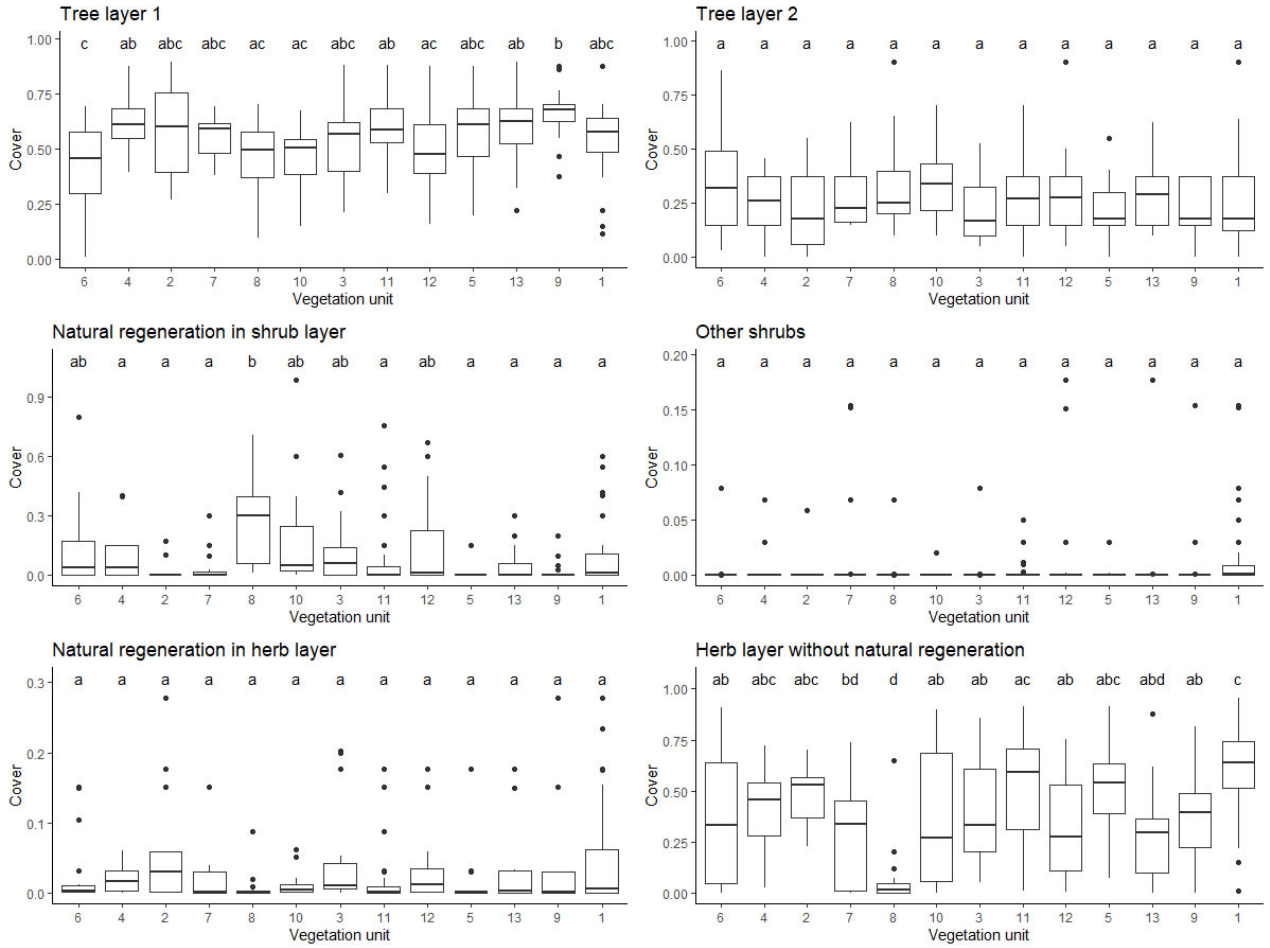

Fig. 9: Boxplot and Tukey test showing the cover of tree layer 1, tree layer 2, natural regeneration in the shrub layer, other shrubs, natural regeneration in the herb layer, and the herb layer without natural regeneration across the 13 forest types.

Abb. 9: *Boxplot und Tukey-Test der Deckung der Baumschicht 1, Baumschicht 2, natürliche Verjüngung in der Strauchschicht, andere Sträucher, natürliche Verjüngung in der Krautschicht, Krautschicht ohne natürliche Verjüngung in den 13 Vegetationseinheiten.*

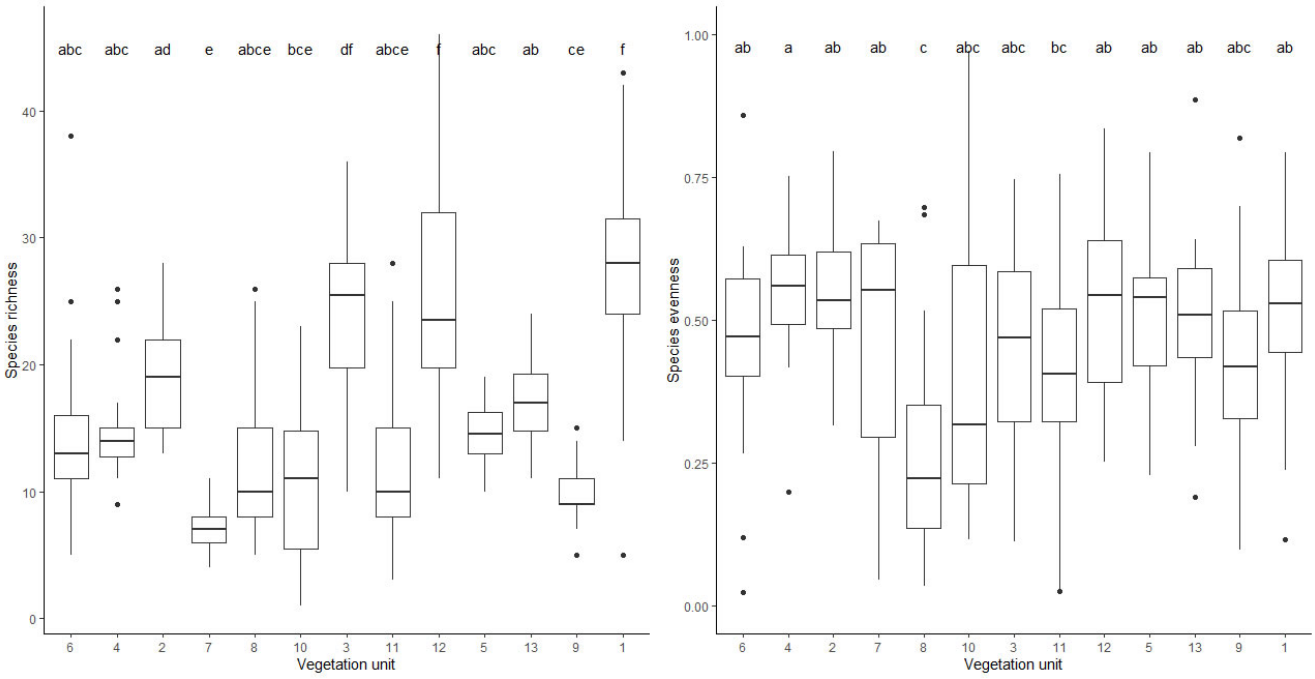

Fig. 10: Boxplot and Tukey-Test of species richness and species evenness across forest types (for legend, see Figure 9).

Abb. 10: *Boxplot und Tukey-Test der Artenanzahl und Evenness in den Vegetationseinheiten (Legende siehe Abb. 9).*

- In forest type 11 features beech (40%), oak (19%), and hornbeam (15%) in the tree layer; however, apart from the *Fagion sylvaticae* species mentioned above, no specific species are present in the understory.
- Forest type 12 is dominated by beech (44%). oak (13%), and hornbeam (11%) with *Urtica dioica* indicating nutrient-rich conditions.
- Forest type 5 consists mainly of beech (43%) admixed with oak (19%) and hornbeam (15%). Species like *Impatiens noli-tangere, Epilobium montanum, Scrophularia nodosa, Galeopsis tetrahit, Moehringia trinervia* and *Mycelis muralis* indicate nutrient-rich conditions.
- Forest types 13 and 9 are dominated by beech (62% and 59%, respectively). Unit 13 has abundant ferns, corresponding to the Melico-Fagetum dryopteridetosum Lohm apud Seib 1954 (= Galio odorati-Fagetum) in Welss (1985) while Type 9 is similar but lacks ferns and is corresponding to the Melico-Fagetum luzuletosum in Welss (1985).

Oak-hornbeam forests (forest type 1):

Forest type 1 comprises oak-hornbeam forests (oak 31%, hornbeam 28%) with beech (16%) as an admixture. Characteristic species of the *Carpinion betuli* alliance such as *Galium sylvaticum, Stellaria holostea* and *Dactylis polygama* are present.

4.2.7 Change of understory species composition

Only 51 out of the 151 plots retained their original forest type affiliation over the three decades. The evaluation of the confusion matrix (Tab. 1) reveals several key findings. The diagonal values represent relevés that remained in the same forest type from 1985 to 2016. High diagonal values indicate constance within certain forest types. In relation to a specific type, the relevés can be classified into three groups: constant relevés, which belong to the same group in both years and show little change in species composition; newcomers, which joined the group in 2016; and leaving relevés, which were reassigned to a different group. For example, in forest type 6, eight out of the original nine relevés remained constant, eight joined and one left the group. Overall, the matrix highlights the dynamic nature of understory vegetation over time, with certain types becoming more prevalent while others decline or shift in composition.

Tab. 1: Confusion matrix of relevé assignment to forest types in 1985 and 2016 in the understory. The relevés on the diagonal are the "constant" relevés. Off-diagonal relevés in the columns are the "newcomers", while off-diagonal relevés in the rows are the "changing" relevés. n85: number of relevés in 1985, n16: number of relevés in 2016, n85&16: group size in both years, Δ: number of changing relevés; Δn: change in group size.

Tab. 1: *Kreuztabelle der Aufnahmezugehörigkeit zu den Vegetationstypen in 1985 und 2016 im Unterwuchs. Zeilen entsprechen 1985, Spalten 2016. Die Relevés auf der Diagonale sind die „konstanten" Relevés. Off-Diagonale Relevés in den Spalten sind die „Neuzugänge", während Off-Diagonale Relevés in den Zeilen die „veränderten" Relevés darstellen. n85: Anzahl der Aufnahmen in 1985, n16: Anzahl der Aufnahmen in 2016, n85&16: Gruppengröße in beiden Jahren (= n85 + n16), Δ: Anzahl der Aufnahmen, die die Gruppenzugehörigkeit geändert haben, Δn: Änderung der Gruppengröße.*

		2016															
	Type	**6**	**4**	**2**	**7**	**8**	**10**	**3**	**11**	**12**	**5**	**13**	**9**	**1**	**n85**	**n85&16**	**Δ**
1985	6	8				1									9	25	-1
	4	1	6			5		1							13	24	-7
	2	1	2	1	1			5	1					1	12	13	-11
	7	1			5	2	2								10	18	-5
	8														0	19	
	10														0	18	
	3						1		1						2	22	-2
	11	1					4	3	7	5					20	35	-13
	12					3			1	7		1			12	32	-5
	5	1				1	6	7		2		1	2		20	20	-20
	13	2				3				4		2			11	16	-9
	9	1	3		2	4	5	1	3	1		1	1		22	25	-21
	1							3	2	1				14	20	35	-6
	n16	16	11	1	8	19	18	20	15	20	0	5	3	15			
	Δn	7	-2	-11	-2	19	18	18	-5	8	-20	-6	-19	-5			

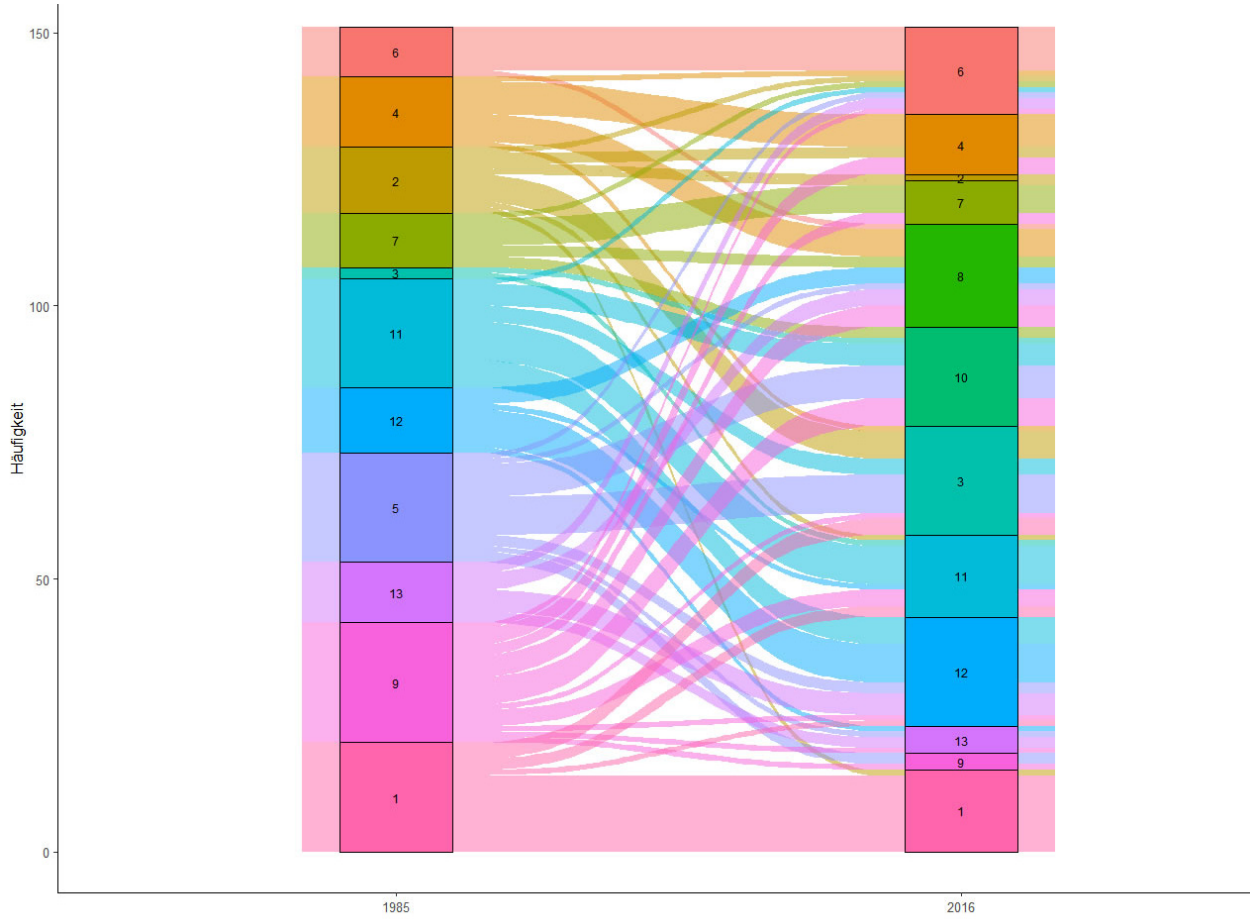

Fig. 11: Sankey diagram showing the change of forest type affiliation in the understory; left: affiliation in 1986, right: affiliation in 2016; bands indicate the change; the order from top (forest type 6) to bottom (forest type 1) follows the order in the dendrogram (Figure 7) from left to right. Only forest types 6 (beech forests) and 1 (oak-hornbeam forests) remained nearly unchanged.

Abb. 11: *Sankey-Diagramm zur Darstellung der Veränderung der Vegetationseinheit-Zugehörigkeit in der Unterschicht; links: Zugehörigkeit 1986, rechts: Zugehörigkeit 2016; die Bänder zeigen die Veränderung an; die Reihenfolge von oben (Vegetationseinheit 6) nach unten (Vegetationseinheit 1) folgt der Reihenfolge im Dendrogramm (Abb. 7) von links nach rechts. Nur die Vegetationseinheiten 6 (Mischbuchenwälder) und 1 (Eichen-Hainbuchenwälder) blieben nahezu unverändert.*

The Sankey diagram (Fig. 11) provides a clear visualization of the shifts provided in Table 1. On the left side, the forest types from 1985 are displayed, with the width of each coloured band representing the number of relevés associated with each unit. On the right side, the forest types from 2016 are shown similarly, with the coloured bands representing the sample size of each unit after the transition. The connections between the left and right sides illustrate how relevés shifted between units over time, with consistent colours making it easy to track these transitions.

Forest types 6 and 1 show minimal changes over time. The widths of the bands connecting these units remain almost identical between 1985 and 2016, indicating that most of the relevés within these units remained stable. In contrast, Units 5, 9, and 2 experienced the most significant declines. The wide bands on the left side in 1985 become much narrower or even disappear on the right side in 2016, demonstrating that these units lost many of their original relevés. Units 8, 10, and 3 display the opposite trend, gaining many relevés over time. The multi-coloured bands feeding into these units indicate that the relevés came from various forest types in 1985, reflecting the dynamic nature of vegetation changes.

Units like 8 and 10 are composed of relevés from multiple different units in 1985, as seen in the various colours converging into a single unit on the right side. This highlights the complexity of the transitions and the merging of relevés from different origins. Forest type 5, which had a substantial presence in 1985, completely disappeared by 2016, while Unit 10 emerged as a new unit, gathering relevés from previously distinct units like 5, 9, and 11.

Forest types 11 and 12 exhibit partial constance. While some relevés remained within these units, others shifted to different units or were newly added. This is reflected in the partially retained bands alongside incoming or outgoing connections.

In summary, the Sankey diagram effectively demonstrates the dynamics of vegetation change over time. Some units, like 6 and 1, show strong constance, while others, such as 5 and 9, underwent significant restructuring or even disappeared. The emergence of new units like 8 and 10 illustrates how shifts in species composition and environmental factors can lead to the reorganization of forest types. This visualization is particularly useful for identifying which forest types remained constance and which underwent major changes,

as well as for understanding the origins of new forest types. Dynamic changes in species composition of the understory and changes in layer cover across forest types over a 34-year period revealed significant shifts. Detailed findings are presented in Appendix 3.

4.2.8 Management impact

The dendrogram (Fig. 12) displays four groups (D, C, A, B) classified based on the frequency of stumps in different stages of decay, each representing clusters of plots with similar stump decay characteristics that reflect the timing of management activities. By classifying the plots according to stump decay stages, we can infer the frequency and intensity of past management practices. Groups with predominantly younger decay stages suggest more recent, intensive, or frequent interventions, while groups with older decay stages reflect less frequent or long-past interventions. The varying decay stages of stumps across the groups illustrate the enduring impacts of management activities on vegetation dynamics. Stumps in advanced decay stages may be associated with less disturbed plant communities, whereas younger stumps indicate ongoing changes and dynamic vegetation processes. The dendrogram reveals a clear sequence of stump decay stages, representing a timeline of management interventions. From right to left, it transitions from more recent interventions (with “recently dead” and “weakly decayed” stumps) to older interventions or natural decay (with “very decayed” and “almost decomposed” stumps).

Group A (Green, second from the right): This group includes stumps ranging from „recently dead“ to „weakly decayed“, and also features „medium decayed“ stumps, suggesting that the plots in this group have experienced a mix of recent and intermediate interventions.

Group B (Blue, far right): Predominantly composed of „medium decayed“ stumps, this group indicates that management activities, such as tree cutting, occurred a moderate time ago. The stumps are neither fresh nor fully decomposed, suggesting an intermediate timespan since the last intervention.

Group C (Red, second from the left): This group has a predominance of „very decayed“ stumps, indicating that management activities took place longer ago, allowing significant stump decay.

Group D (Black, far left): Characterized by the highest proportion of „almost decomposed“ stumps, this group suggests that interventions either occurred a very long time ago or that the stumps have undergone extensive natural decomposition, reflecting the oldest or least frequent interventions among the groups.

Only a few species showed significant changes in cover between 1985 and 2016 within these management groups (Tab. 2). *Fagus sylvatica* in the shrub layer increased across all management categories, with the most substantial growth observed in plots harvested further in the past (Groups C and D). Conversely, *Galium odoratum* experienced the greatest decline in these same categories (C and D), indicating a shift in species composition over time. *Vaccinium myrtillus* declined primarily in recently harvested plots (Groups A, B, and C), reflecting the immediate impact of recent management practices on this species.

From 1985 to 2016, there were no significant differences in changes in species richness, species evenness, or cover of tree, shrub, and herb layers within the four management groups (Kruskal-Wallis-Test, $p > 0.05$).

Comparing plots with and without skid trails revealed no significant difference in herb layer cover change ($t = 0.24$, $p = 0.81$; Wilcoxon $W = 2453$, $p = 0.82$). Mean changes in herb cover were nearly identical in both plot types (−0.27 vs. −0.28).

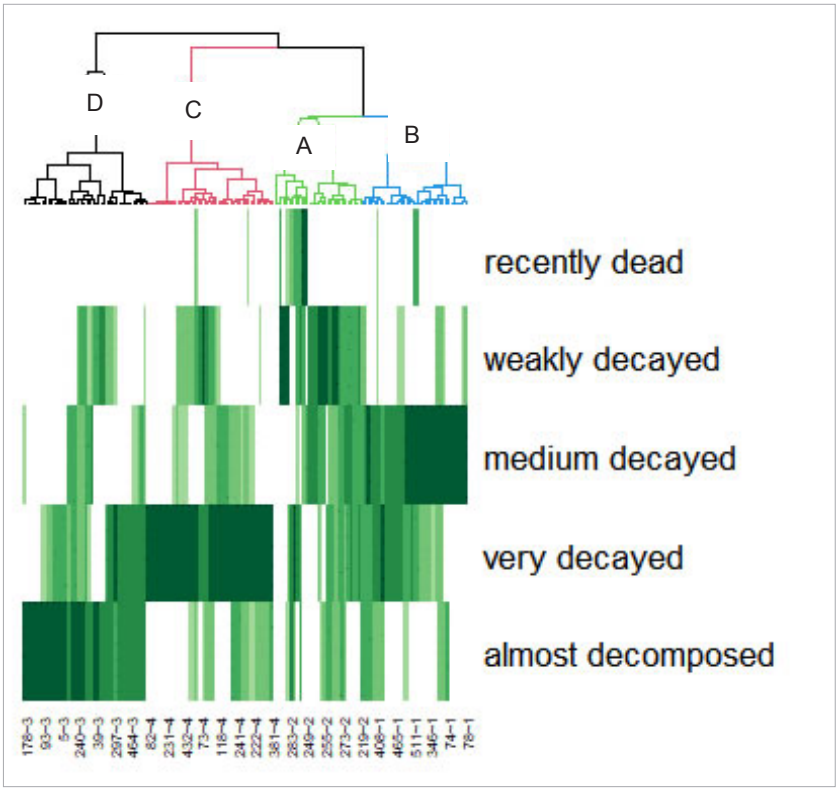

Fig. 12: Dendrogram showing the classification of plots based on decay stage and the number of thumbs. The darker the green, the more thumbs are present in the plot.

Abb. 12: *Dendrogramm zur Klassifikation der Plots basierend auf dem Zersetzungszustand und der Anzahl der Baumstümpfe. Je dunkler das Grün, desto mehr Baumstümpfe des jeweiligen Zersetzungsgrades sind vorhanden.*

Tab. 2: Management groups (A, B, C, D): Species of understory vegetation changing cover values significantly (H: Herb layer, S: Shrub layer); A recently cut, B and C intermediary, D cut in the past.

Tab. 2: *Managementgruppen (A, B, C, D): Arten des Unterwuchses mit signifikanten Deckungsunterschieden (H: Krautschicht, S: Strauchschicht); A: kürzlich geerntet, B und C dazwischenliegend, D Erntetermin liegt länger zurück.*

		Management group			
	Layer	**A**	**B**	**C**	**D**
Fagus sylvatica	S	9.70	5.39	14.12	15.72
Tilia platyphyllos	S	0.00	0.00	0.00	0.14
Bromus benekenii	H	0.00	-0.42	0.00	-0.08
Calamagrostis arundinacea	H	-2.10	-0.38	-1.75	-1.67
Carex sylvatica	H	0.20	0.07	-0.42	-0.55
Festuca ovina	H	-1.38	-0.26	-0.01	0.00
Galium odoratum	H	-2.86	0.11	-7.56	-9.16
Lapsana communis	H	0.01	0.00	-0.35	0.00
Lathyrus linifolius	H	-0.02	-0.35	-0.01	0.02
Melica nutans	H	-0.01	0.00	-0.08	0.00
Scrophularia nodosa	H	0.03	-0.01	-0.03	-0.01
Vaccinium myrtillus	H	-5.36	-1.68	-8.19	0.19

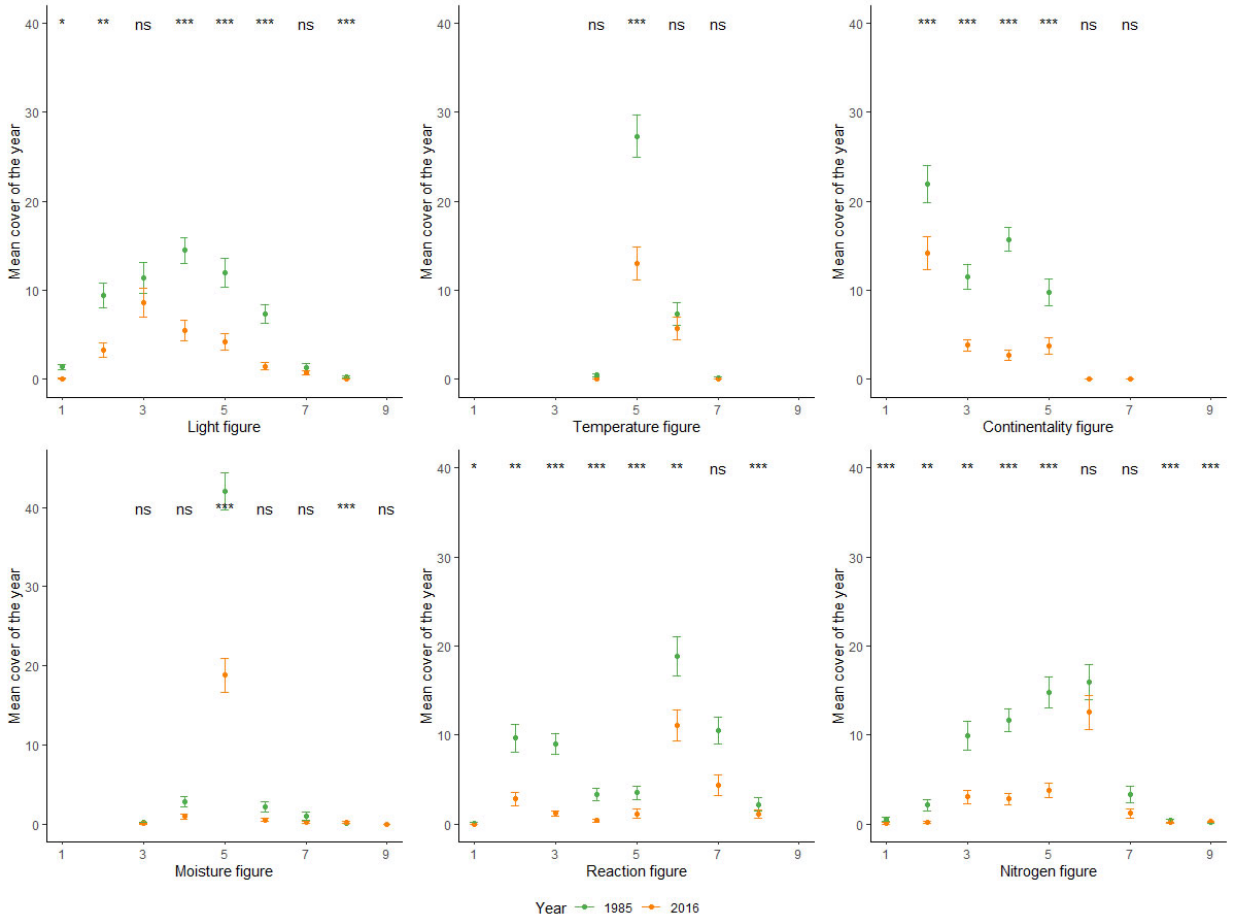

Fig. 13: Spectra of Ellenberg indicator values for 1985 and 2016, with mean cover and error bars (standard errors) shown for each year. The Wilcoxon test was used to compare the categories between the years. *: p < 0.05; **: p < 0.01; ***: p < 0.001; ns: p > 0.05.

Abb. 13: *Zeigerwertspektren für 1985 und 2016. Mittlere Deckung und Fehlerbalken (Standardfehler) für jedes Jahr. Wilcoxon-Test der einzelnen Kategorien, um signifikante Unterschiede zwischen den Jahren zu finden. *: p < 0.05; **: p < 0.01; ***: p < 0.001; ns: p > 0.05.*

4.3 Main drivers of change

The average cover (median) of the herb layer decreased from 55% in 1985 to 16% in 2016. This significant change indicates that site conditions altered during the observation period, leading to this reduction in herb layer cover.

4.3.1 Indicator values and life forms

The analysis of mean values for Ellenberg indicator values shows no significant changes between the years, except for the nitrogen figure, which increased from 4.7 to 5.0.

The analysis of the spectra of Ellenberg indicator values indicates that, in general, all spectra have a similar shape when comparing 1985 and 2016, but there is a marked decline in mean cover values over this period (Fig. 13).

For the light figure, the maximum shifted from 4 to 3. This shift is primarily due to a significant decrease in species with light figures of 4, 5, and 6. The temperature figure was predominantly associated with a value of 5 ("fairly warm conditions, from lowland to montane," (Ellenberg et al. 2001)). The continentality figure shows a complex pattern: the dominant value is 2 ("oceanic, mainly in the West, including western Central Europe"), with the largest decline seen in species with a value of 4 ("suboceanic, mainly in Central Europe, but spreading eastward"). For the moisture figure, nearly all species in both record years had a value of 5, indicating intermediate conditions, but there was a strong decline in mean cover from 40% to less than 20%. The soil acidity figure exhibits a bimodal distribution with a wide range of values in both years, reflecting the heterogeneous geology of the area. The nitrogen figure showed a significant decline for species with values of 3 to 5, indicating a loss of species cover associated with poor to intermediate soil conditions.

All Raunkiaer life forms declined in cover (Fig. 14), with hemicryptophytes (plants with hibernating buds near the soil surface) being the most affected.

4.3.2 Changing climatic parameters

From the nearby in Ebrach located climate station of the German Weather Broadcast Service (Deutscher Wetterdienst, DWD) detailed climatic data for the study region are available starting in 1963. "Mean annual temperature" rises with a rate of 2.9K/100a from 7.3°C in 1963 (when they started measuring at this station) to 9.0°C today (2021, Fig.15).

The number of "cold days" as well as the number of "frost days" decreased, while the number of "warm days" increased. Extreme temperature values like "absolute minimum" and "absolute maximum" both increased, indicating that it is getting warmer in both summer and winter (Appendix 4).

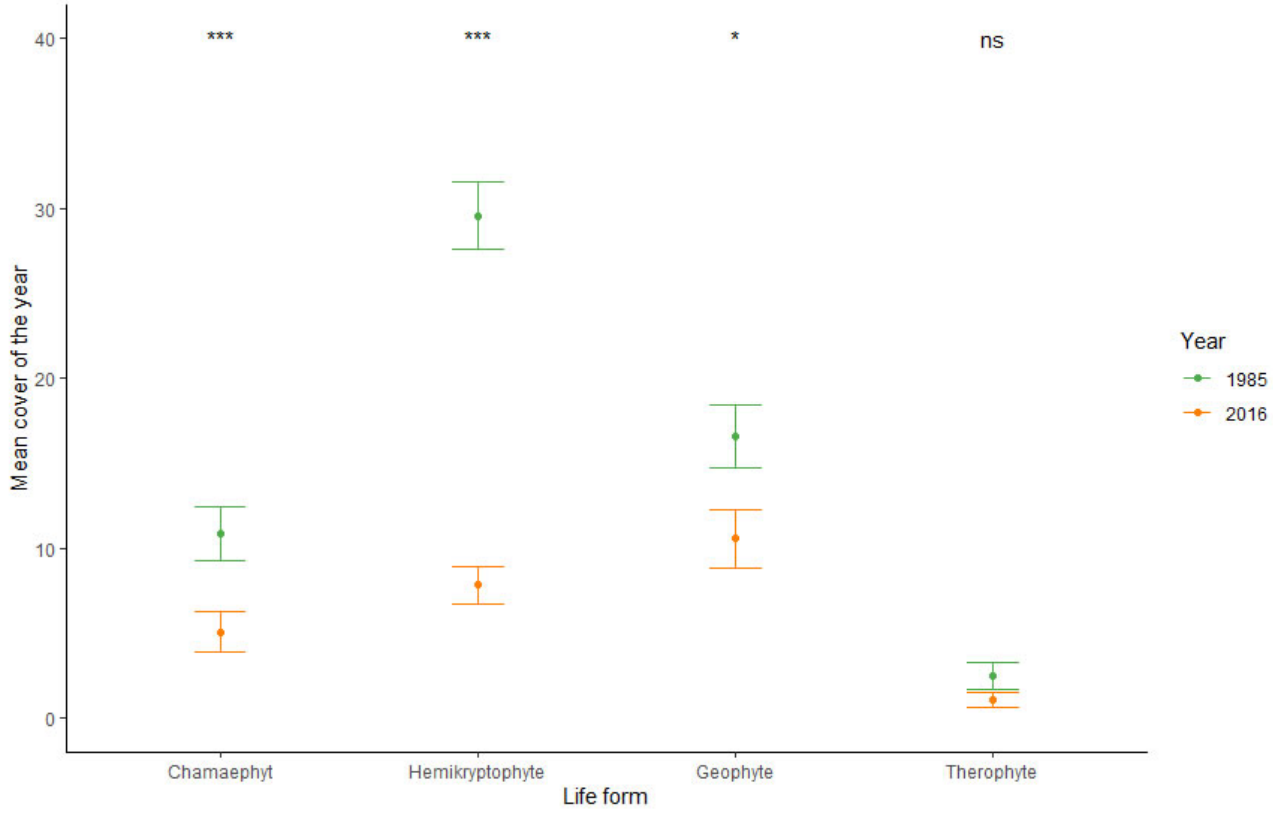

Fig. 14: Spectra of life forms for 1985 and 2016, with mean cover and error bars (standard errors) shown for each year. The Wilcoxon test was used to compare the categories between the years. *: p < 0.05; **: p < 0.01; ***: p < 0.001; ns: p > 0.05.

Abb. 14: *Lebensformenspektren für 1985 und 2016. Mittlere Deckung und Fehlerbalken (Standardfehler) für jedes Jahr. Wilcoxon-Test der einzelnen Kategorien, um signifikante Unterschiede zwischen den Jahren zu finden. *: p < 0.05; **: p < 0.01; ***: p < 0.001; n.s: p > 0.05.*

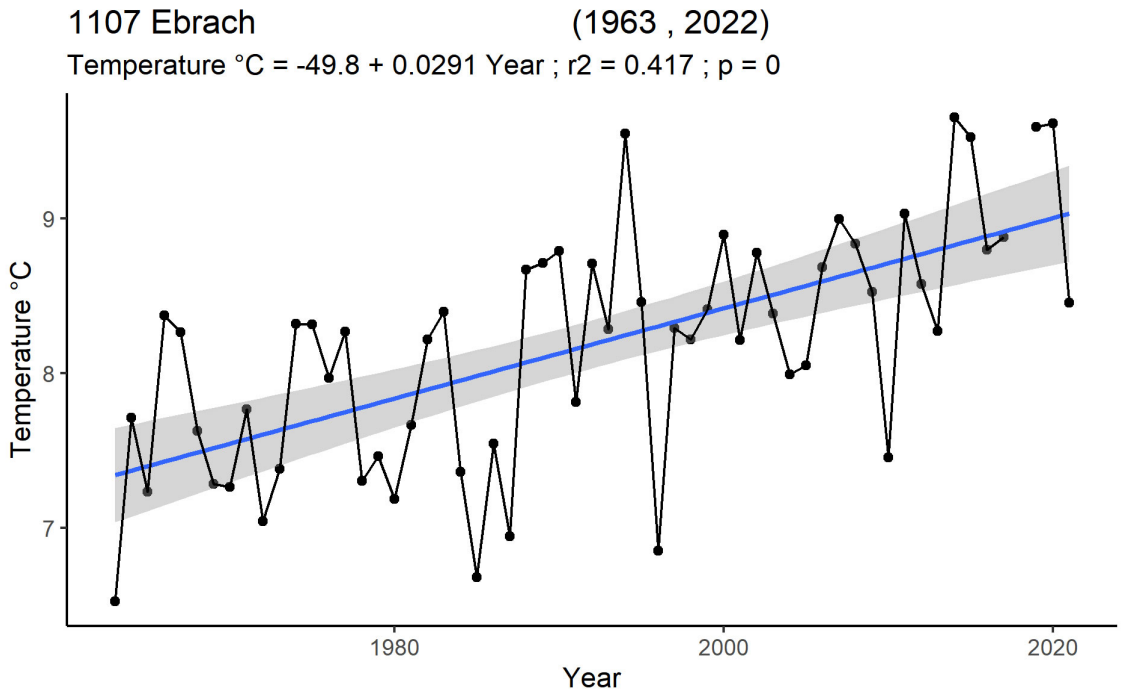

Fig. 15: Mean annual temperature at the climatic station Ebrach. Mean of daily mean of temperature at 2m height, data source: www.dwd.de.

Abb. 15: *Mittlere Jahrestemperatur an der Wetterstation Ebrach. Mittelwerte der Tagesmittel in 2 m Höhe, Datenquelle: www.dwd.de.*

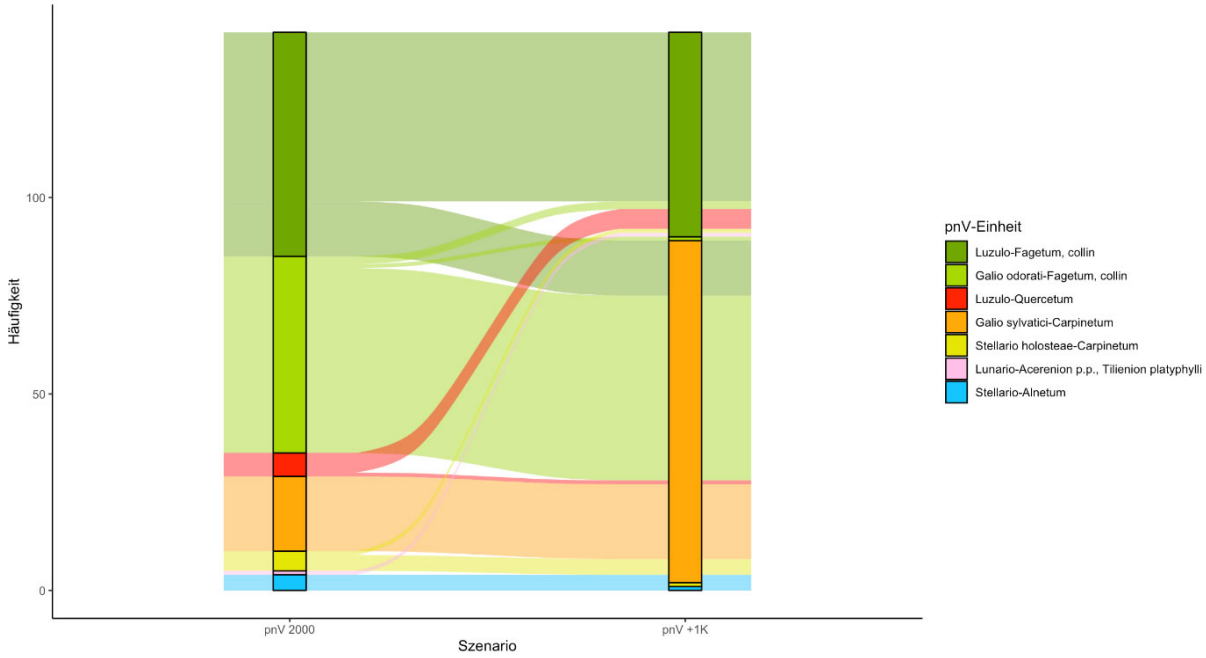

Fig. 16: Frequency distribution of PNV units in the 151 plots in the year 2000 (left) and in the scenario +1K (right). Based on climate data 1971–2000 and soil data.,Fischer et al. (2019).

Abb. 16: *Häufigkeitsverteilung der PNV-Einheiten in den 151 Aufnahmen in der heutigen PNV im Jahr 2000 (links) und in der zukünftigen PNV: Szenarium +1K, rechts. Basierend auf Klimadaten 1971–2000 und Bodendaten, Fischer et al. (2019).*

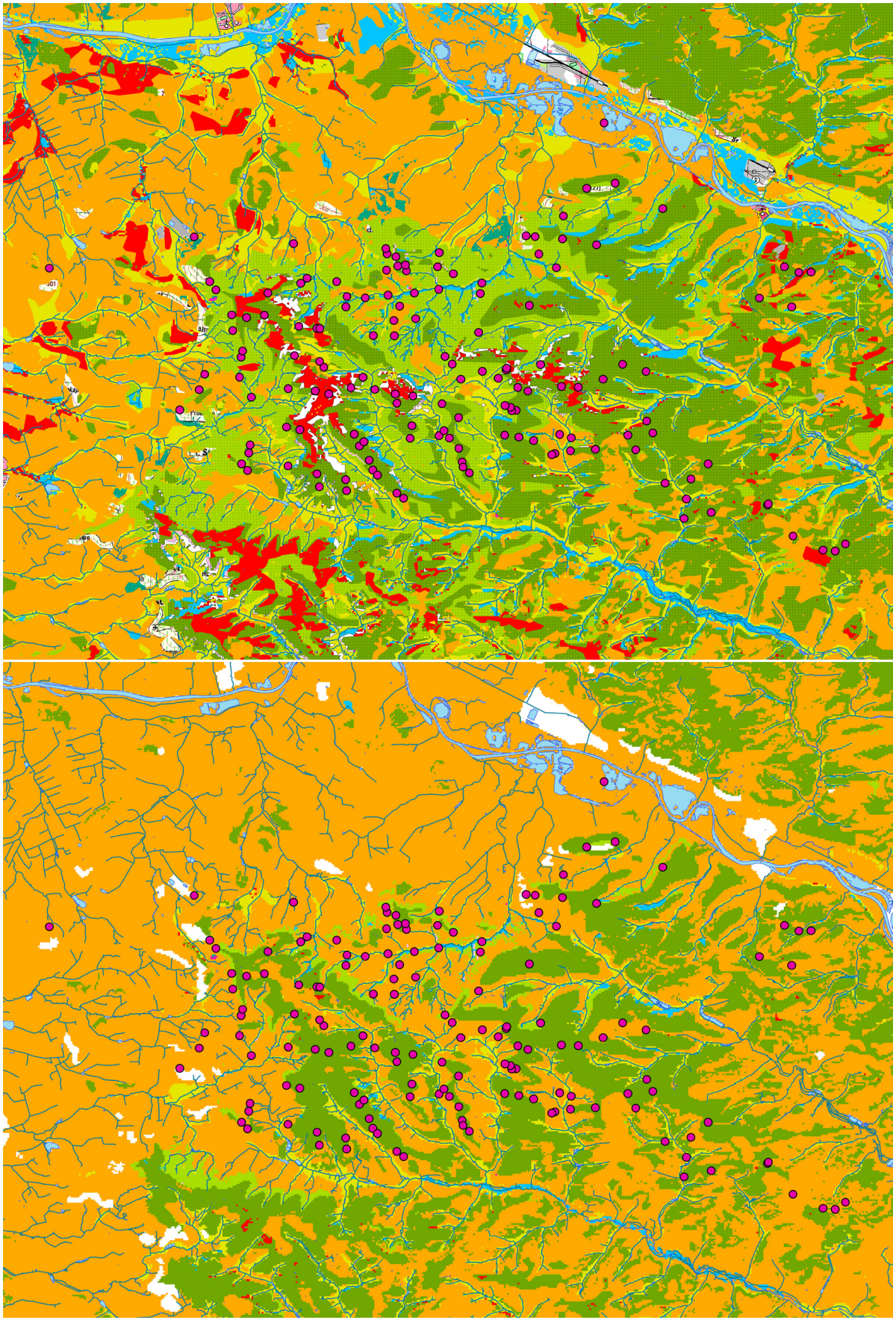

Fig. 17: Map of the current (2000 top: climate data 1971–2000; FISCHER et al. 2019) and future (bottom) PNV (+1K). Points indicate the location of the sample plots. For the legend, see Figure 16.

Abb. 17: *Karte der heutigen (2000, oben, Klimadaten 1971–2000, FISCHER et al. 2019) und zukünftigen (unten) PNV (+1K). Punkte zeigen die Lage der Aufnahmeflächen. Legende siehe Abb. 16.*

4.3.3 Potential Natural Vegetation

The mean annual temperature in the Steigerwald region has increased by 1.7K from 1964 to 2021. The Sankey diagram (Fig. 16) illustrates the impact of this climate change on the potential natural vegetation (PNV) of the plots. A detailed map of the PNV of Bavaria of the year 2000 is available from Fischer et al. (2019), (Fig. 17). In the year 2000, the PNV was relatively diverse, with seven different forest types represented in the plots, including the main types: Luzulo-Fagetum, collin, Galio odorati-Fagetum, collin, Luzulo-Quercetum, and Stellario-Carpinetum (Oberdorfer 1957). This diversity reflects the forest types outlined in Appendix 3.

However, in the "+1K scenario," which simulates an additional temperature increase of 1K, the forest composition becomes much more uniform, with primarily two forest types extending. The forest type Galio-Carpinetum becomes almost exclusively dominant, while the acidic beech forest type (Luzulo-Fagetum) decreases slightly. The types Galio odorati-Fagetum and Luzulo-Quercetum nearly disappear. Consequently, the PNV map for the study area shows a dramatic change (Figure 17), indicating a significant reduction in forest diversity and a shift toward to forest types better adapted to the warmer conditions (Galio-Carpinetum).

5 Discussion

Long-term vegetation surveys, such as this study in the Steigerwald region of northern Bavaria, offer crucial insights into forest dynamics over extended periods. By re-surveying historical relevés at the same locations, this research adds to the growing body of literature on shifts in floristic composition across Central European forests (e.g., Röder et al. 1996, Jantsch et al. 2013, 2014, Bernhardt-Römermann et al. 2015, Schmidt & Heinrichs 2017, Dierschke & Becker 2020, Günther et al. 2021, Staubli et al. 2021, Jandt et al. 2022). A key strength of this study is its use of over three decades of resurvey data, collected using consistent methods, and with the same researcher involved in the relevés, reducing variability and increasing the reliability of the findings.

The changes observed in the study area over the past three decades will be discussed here under the following aspects:

5.1 Cover changes across layers

Regarding tree species cover, we observed a slight decrease in the upper tree layer, a slight increase in the lower tree layer, and a moderate increase in the shrub layer. The cover of natural regeneration in the herb layer remained relatively stable. In contrast, the cover of herbaceous species declined drastically, dropping from 55% to 16%. The overall woody layer (comprising trees and shrubs) increased slightly from 68% to 72%, with only minor changes in the tree and shrub layers. Notably, shading from tree and shrub layers accounted for only a small portion of the significant decline observed in the herb layer (Fig. 2). Our analysis showed that the sampling year explained 23% of the variance in herb layer cover, compared to just 4% explained by shading from woody layers, indicating that other factors than denser woody layer are driving this decline.

In contrast to our findings, Dierschke & Becker (2020) did not report notable changes in the cover of understory vegetation over a 36-year observation period. On the other hand, Kyaschenko et al. (2022), examining biodiversity-oriented management in Swedish forests, observed significant decline in the understory vegetation cover, particularly in the herb layer without natural regeneration. Their results indicated a decrease in understory vegetation cover over three decades. They attributed this decline primarily to reduced light availability caused by a denser forest overstory. Depauw et al. (2020) found that the composition of the herb layer in semi-natural deciduous forests is primarily influenced by local canopy characteristics, which regulate light availability at the forest floor, while broader environmental factors, such as warming, nitrogen deposition, and aridity, play a considerably smaller role at the regional scale.

In contrast, our findings from the Steigerwald study documented a significant decline in herb layer cover, while this reduction was *not* linked to increased canopy density. Staubli et al. (2021) reported a significant reduction in herb layer cover by 20% (from 60% to 40%), with no significant changes in tree and shrub coverage. They attributed the decline to the severe summer drought of 2018. Consistent with these observations, we believe that drought conditions, particularly those experienced in 2015, provide the most plausible explanation for the drastic decline in herb layer biomass in our study. This is further supported by Wachtveitl et al. (2024), who published data from the Bavarian Intensive Forest Monitoring plot Ebrach (level II). They reported that the deviation from the mean climatic water balance (1995–2022) in 2015 was extremely negative, at -220 mm. The average summer precipitation amounted to 342 mm. This deficit indicates that the water balance was 220 mm below the long-term average, potentially due to lower precipitation or increased evapotranspiration. During the summer of 2015, beech trees experienced a 43% loss of foliage due to crown thinning, creating conditions that were both lighter and drier in the herb layer.

As a consequence, there are several reasons for a decrease in herb layer cover beyond a denser tree canopy. In the Steigerwald increasing drought seems to be a main driving force for this kind of vegetation change.

5.2 Species dynamics

Overall, the species composition of the tree layer showed only minimal changes between 1985 and 2016. Beech (*Fagus sylvatica*) was present in nearly all relevés in both years, commonly mixed with sessile oak (*Quercus petraea*), hornbeam (*Carpinus betulus*), and occasionally conifers such as Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and European larch (*Larix decidua*). The only notable change in the overstory was a slight increase in *Sorbus torminalis,* a species that favours warmer conditions. The Sankey diagram shows that 53% of the plots retained their group affiliation, highlighting the high stability in tree layer composition. The minor shifts observed mainly occurred in plots with conifers, reflecting management efforts to reduce non-native conifers in favour of site-adapted species.

Species richness and evenness in the herb layer remained constance between 1985 and 2016, suggesting that overall diversity metrics were not drastically altered despite shifts in species composition.

Dierschke & Becker (2020) reported a slim decrease in species richness from 63 to 58 species in a transect with 41 plots, located in a fenced experimental area without forest management. As the main driver for vegetation changes the forest history is considered, i.e. the change from a coppice-with-standards to high forest. Heinrichs et al. (2023) reported a decrease in species richness. Bernhardt-Römermann et al. (2015) conducted a meta-analysis of 39 resurvey studies in temperate forests across Europe to identify the key environmental factors influencing temporal changes in plant diversity. They found no overall net loss in local species diversity, such as species richness or evenness, but observed significant variation among sites, in most datasets, species' diversity either increased or decreased with time. The variation was partly explained by temporal changes in light availability, which acted as a local driver, and the density of large herbivores, which served as a regional driver. Helm et al. (2017) resurveyed 179 plots in mixed mountain forests in the Northern Calcareous Alps, Austria, and observed a decline in total species richness from 235 to 207 species. They attributed this decrease to the interaction of large-scale environmental changes (such as climate change and air pollution) with local pressures that affect plots differently, primarily changes in the tree canopy. Jandt et al. (2022) analysed 7,738 vegetation plots across Germany, including forests, grasslands, and mires, and reported a minor decrease in species richness. Our findings in the Steigerwald demonstrate that forest management emphasizes promoting the natural regeneration of tree species. This approach includes maintaining a low deer population, which is evident in the successful regeneration of tree species within the herb and shrub layers. Furthermore, our observations suggest that close-to-nature management practices contribute to biodiversity conservation, as they preserve species richness in the understory vegetation.

Significant changes in overall species cover were observed: 21 species increased in cover, while 55 species decreased. Species such as *Fagus sylvatica* (shrub layer), *Rubus fruticosus agg, Impatiens parviflora, Urtica dioica,* and *Galium aparine* showed increases in cover and frequency, whereas others, including *Luzula luzuloides* and *Galium odoratum,* declined. Günther et al. (2021) reported a similar pattern in the herb layer, with numerous species experiencing losses in cover and only a few showing gains. Jandt et al. (2022) found that losses in species cover were more common than gains, leading to biotic homogenization driven by the spread of generalist species – a trend observed broadly across various ecosystems. Similarly, the Steigerwald study, which focused specifically on forest ecosystems, observed increases in generalist species and declines in forest specialists. However, unlike the findings of Jandt et al. (2022), the Steigerwald study also highlighted successful natural regeneration of tree species like *Fagus sylvatica, Acer platanoides, Acer pseudoplatanus, Carpinus betulus, Tilia cordata, Sorbus torminalis,* which aligns with the goals of close-to-nature forest management. This comparison underscores shared trends of homogenization while also highlighting the unique success of natural regeneration in the Steigerwald.

The correspondence analysis revealed that the understory species composition has become increasingly homogeneous over time, whereas the tree layer did not exhibit this trend. This suggests that changes in tree layer composition are not driving the observed shifts in the understory. Similarly, Naaf & Wulf (2010) reported herb layer homogenization driven by the spread of native species tolerant of a wide range of pH and moisture conditions. Helm et al. (2017) identified thermophilization and drying as key drivers of understory changes in mixed mountain forests in Austria. These findings align with our observations of increasing similarity among understory plots in the Steigerwald. Schmidt & Heinrichs (2017) attributed vegetation homogenization to increasing eutrophication, supported by shifts in nitrogen indicator values and direct measurements of nitrogen deposition. While the critical load for nitrogen deposition in Central European deciduous forests is slightly above 10kg/ha/year (Buriánek et al. 2013), levels in the Steigerwald reach up to 20kg/ha/year (Raspe et al. 2018). Despite this, we did not observe a major increase in nitrogen-demanding species, as reported by Bernhardt (2005). Instead, the decline in cover spans species with both low and high nitrogen indicator values. This indicates that while nitrogen deposition contributes to homogenization, other factors, such as drought, also play a significant role. Hédl et al. (2017) emphasized the long-term effects of former management practices, such as coppicing, on current forest structure and species composition. In the Steigerwald, forest management transitioned from coppice-with-standards in the 16th century to high forest management in the 19th century, with a focus on beech timber from 1900 onwards (Sperber 2014, Mergner et al. 2020). Since 1972, close-to-nature forestry has been practiced. While historical management undoubtedly influenced forest structure, our findings suggest that contemporary changes, such as the decline in the herb layer, are more likely driven by environmental stressors like drought and nitrogen deposition rather than past management practices.

The numerical classification of relevés from 2016 revealed the same main forest types identified in Welss (1985): *Luzulo-Fagion, Quercion roboris, Fagion sylvaticae*. This highlights the continuity of the dominant ecosystem structures over time. However, a closer examination reveals notable dynamics in the species composition of the understory. These changes primarily affect beech forests on base-rich soils (*Fagion sylvaticae*), with some forest types disappearing completely and new types emerging. This has led to forest types with sparse cover and limited natural regeneration in the herb layer, alongside moderate regeneration in the shrub layer.

Luzulo-Fagion and *Carpinion betuli* seem to be relatively constance, while oak forests (*Quercion roboris*) on acidic, poor soils have significantly decreased, with many converting to *Fagion sylvaticae* forests. This shift may be due to soil recovery from acid rain (Wellbrock et al. 2016) while other conversions to acidic beech forests (*Luzulo-Fagion*) reflect a natural succession from oak plantations to beech forests.

The species composition of the tree layer remained largely unchanged between observation years, making it unlikely that changes in the tree layer are responsible for the observed fluctuations in the herb layer. This raises the question of what other factors might be contributing to these changes. Verheyen et al. (2012) found that the shift toward denser canopies with more shade-casting species and more decomposable litter was a major driver of changes in understory composition, rather than nitrogen deposition alone. Increased canopy density typically results in darker conditions for understory plants; however, our data showed no significant shift in Ellenberg light values towards "darker" conditions, nor did the canopy layer show notable changes in total woody cover. Moreover, the Nationwide Forest Condition Survey (BMEL 2024) reports

that beech trees experienced an average crown thinning of about 15% in 1985, which increased to approximately 28% in 2016 and 2023. As of 2023, only 15% of beech stands showed no crown thinning. For oak, crown thinning was 17.5% in 1985, 21.4% in 2016, and 27.6% in 2023, with only 17% of areas showing no crown thinning. Mergner et al. (2020) also reported severe crown thinning and dieback in beech trees in the Steigerwald following the droughts in 2015, 2018 and 2019. This indicates that canopies in the study area are becoming rather lighter than denser, particularly in managed forests, contradicting the assumption that increased shading is driving the observed strong understory changes.

Our findings are consistent with other studies on forest vegetation dynamics in Central Europe, which report shifts in species composition and declines in herb layer diversity due to changing environmental conditions (Hédl et al. 2017, Günther et al. 2021). The reduction in herb layer cover observed in the Steigerwald mirrors trends in other regions, indicating that broader environmental factors such as rising temperatures and altered precipitation patterns are key drivers of these changes (Senf et al. 2020). The constance of species composition in the overstory compared to dynamic changes in the understory highlights the differential sensitivity of vegetation layers to environmental drivers (Fischer et al. 2015). Helm et al. (2017) found similar patterns in mixed mountain forests in the Northern Calcareous Alps, attributing understory changes to thermophilization and drying, which further supports the idea that warming and drying conditions significantly influence understory dynamics, contributing to homogenization and declines in herb layer cover.

5.3 Impact of management practices

All plots included in this study have undergone regular thinning as part of the standard silvicultural regime practiced in the Ebrach Forest District. While thinning intensity varies among plots, our analyses show that changes in vegetation dynamics – particularly the decline in herb layer cover – occurred consistently across all intensity levels. This suggests that the extent of thinning is not significantly correlated with herb layer decline.

Furthermore, our tests comparing plots with and without skid trails revealed no statistically significant differences in herb layer cover change between the two groups. This is particularly noteworthy because skid trails are typically more exposed and subject to elevated soil compaction, light, and desiccation. The lack of a significant difference implies that the widespread loss of forest floor vegetation cannot be attributed to skid trail infrastructure either.

In addition, browsing pressure has remained at moderate levels throughout the observation period. Monitoring data from 124 transects collected between 2012 and 2021 show terminal shoot browsing rates averaging 12.3%, with over 80% of transects falling within acceptable limits (Bayer. StMELF 2018). Consequently, herbivore pressure is unlikely to explain the observed long-term decline in herb layer vegetation.

Although forest management has certainly shaped forest structure over time, our data do not support the conclusion that it is the primary driver of the recent drastic changes in herb layer cover and composition. Rather, the consistent decline across all management categories points to broader environmental stressors – most notably prolonged summer drought and rising temperatures – as the dominant forces behind these changes.

Canopy thinning, while historically used to improve light availability and support regeneration, has likely changed in function under new climatic conditions. As temperatures rise and droughts intensify, thinning may now contribute to increased evaporative demand and soil drying (Thom et al 2023). This suggests a shift from thinning as a regenerative tool to a potential amplifying factor for vegetation stress, particularly in the understory. However, given that thinning has been consistently applied since the 1970s, and all plots are regularly managed, it is the interaction with climate change – not management per se – that appears to drive recent dynamics.

The absence of microclimatic and soil moisture data – both at the time of the original surveys and during the resurveys – limits the precision with which vegetation changes can be linked to environmental drivers. While regional data from the Ebrach forest climate station capture overarching climatic trends, they do not reflect the considerable spatial heterogeneity in soil properties, shading patterns, or hydrological conditions at the plot level. It is likely that macroclimatic changes, particularly increased heat and prolonged summer droughts, have translated into local microenvironmental stress, affecting moisture-sensitive understory species across all management intensities.

To better understand and anticipate such ecosystem responses, future research must combine more spatially resolved environmental monitoring – particularly of soil moisture and microclimatic parameters – with continued long-term vegetation surveys.

5.4 Main drivers to interpret observed changes

To assess the influence of environmental variables, we analysed species composition using Ellenberg indicator values. The spectra showed a strong decline in the cover of indicator species across all figures. For the light indicator, there was a decrease in light-demanding species (values 4 to 6), but no corresponding increase in shade-tolerant species (values 1 to 3), suggesting that the observed decline is not due to increased canopy cover, as the average cover of the woody layer changed only slightly between years. This may also explain why shade-tolerant species have not increased.

For the nitrogen indicator, species that signal poor soil conditions declined the most, while those indicating rich soils did not increase, despite evidence of nutrient input. This suggests that nutrient availability is not translated into higher biomass in the herb layer, possibly due to other limiting factors. For the temperature and moisture indicators, no shifts were observed, even though climate change is ongoing. This is particularly noteworthy given the significant dieback of old beech trees in the Steigerwald since 2019 due to drought and heat (Mergner et al. 2020, Dietrich et al. 2022).

All Raunkiaer life forms showed a decline in cover, with hemicryptophytes being the most affected. This decline is likely due to summer droughts, which impact the buds and hinder their recovery, contributing to the broader reduction in herb layer cover and changes in species composition. The sensitivity of hemicryptophytes to drought stress highlights

their vulnerability to changing moisture conditions, which are exacerbated by ongoing climate change. While drought appears to be a significant factor, the overall reduction in cover across all life forms suggests that multiple environmental stressors, including increased temperatures, may also be contributing to these changes. Further research and data are needed to fully understand the complex interactions affecting these life forms and their role in the broader shifts in vegetation dynamics.

The critical concern is the negative climatic water balance, which directly leads to soil dryness. The increase in mean annual temperatures, along with the decrease in ice and frost days and the rise in warm and hot days, has elevated transpiration rates, thereby reducing soil water availability. A negative climatic water balance indicates drought conditions and soil moisture deficits. This soil dryness is a key factor contributing to the observed decline in the herb layer, changes in understory community composition, and the recent dieback of beech trees in the Steigerwald (Mergner et al. 2020, Dietrich et al. 2022, Wachtveitl et al. 2024). The increasing dryness not only affects plant growth but also influences nutrient cycling and ecosystem resilience, potentially leading to further shifts in species composition and forest structure. While temperature rise and reduced soil moisture are primary drivers, the broader impact of these changes highlights the need for adaptive management strategies, such as enhancing drought resilience through species selection and forest structure adjustments. Spiecker & Kahle (2023) investigated climate-driven tree mortality and growth in the Black Forest, Germany, using a unique and extensive dataset. Over a 68-year period, the study analyses tree mortality, specifically focusing on “desiccated trees,” excluding deaths caused by storm, snow, ice, and fire. The study links this mortality data with a 140-year record of the climatic water balance and a 121-year record of annual radial growth of Norway spruce. The findings show that decreasing climatic water balance, particularly during consecutive hot and dry summers, is strongly associated with increased tree mortality and reduced growth, highlighting a multidecadal impact of drought and heat on forest trees.

The potential natural vegetation (PNV) for the year 2000 identified a range of PNV units at the 151 sampling points, with Luzulo-Fagetum and Galio odorati-Fagetum as dominant types. Under a simulated +1°C climate scenario, a substantial shift is projected: Galio-Carpinetum is expected to expand significantly, replacing most other forest types, while Luzulo-Fagetum largely persists. Between 1985 and 2016, the mean annual temperature in the study area increased from 8.0°C to 8.9°C, leading to a decline in the climatic water balance. A positive water balance supports groundwater recharge, whereas a negative balance induces drought stress in plants, especially on soils with low water-holding capacity, such as sandstone and clay, common in parts of the Steigerwald region. The PNV model (Fischer et al. 2019) indicates that Galio-Fagetum performs optimally at a May-September climatic water balance of 272 mm, whereas Galio sylvatici-Carpinetum thrives at -75 mm. This highlights the susceptibility of Galio-Fagetum to drought stress, favouring the expansion of Galio-Carpinetum under increasingly arid conditions. These projected shifts align with observed changes in understory vegetation, potentially explaining the relative stability of *Carpinion betuli* relevés (group 1). The PNV simulations suggest that further warming could shift forest composition from beech-dominated stands towards hornbeam-oak forests, which are more resilient to drier conditions. This aligns with the observed dieback of older beech trees, emphasizing that continued climate warming could significantly reshape forest ecosystems in the Steigerwald region.

5.5 Explanation of results

The observed changes in the Steigerwald forests, including the decline in herb layer cover and shifts in species composition, are primarily driven by climate change. One of the key factors causing these changes is the climatic water balance. Several aspects, alongside measurements from the Bavarian Intensive Forest Monitoring plot Ebrach (level II) from 2015, are of importance.

Reduced water availability during summer: As summer days and hot days (over 25°C and 30°C) increase, evapotranspiration also rises, creating water deficits. The increase in drought-tolerant species such as *Sorbus torminalis* and the decline of moisture-indicating species such as *Galium odoratum* and *Milium effusum* further suggest a worsening of soil moisture conditions.

Regional temperature increase: Significant changes in the region support this hypothesis, including a rise in mean annual temperature from 7.3°C in 1963 to 9.0°C in 2021, fewer frost days and more summer days and hot days and maximum temperatures exceeding 37°C.

These trends strongly suggest that the climatic water balance – driven by increased evapotranspiration and reduced water availability – plays a key role in the observed vegetation shifts in the Steigerwald. Further analysis of the precipitation-to-evapotranspiration ratio and its correlation with vegetation changes would provide valuable insights.

5.6 Strengths, limitations, and methodological considerations

One of the main strengths of this study is its long-term dataset, which spans over 3 decades. This allows for the detection of gradual ecological changes that shorter studies might miss, providing a robust view of long-term forest dynamics. The resurvey methods, which involved revisiting the same plots, ensure data consistency, making the findings on vegetation structure and species composition highly reliable. Additionally, the study provides a comprehensive analysis of multiple forest layers – tree, shrub, and herb – offering a detailed understanding of how different vegetation layers respond to environmental changes. Another key strength is that the study was conducted in forests managed under close-to-nature principles, providing practical insights into how sustainable forestry interacts with climate impacts.

However, the study has some limitations. As in all region-wide studies the lack of direct microclimatic data and soil moisture or understory humidity, limits the precision in linking climate effects to vegetation changes. Furthermore, disentangling the effects of forest management practices from climate-driven changes is complex. Although the study is able to highlight climate change as the main driver of changes, the role of selective logging and natural regeneration may interact with these climatic factors in ways, that are not fully explored.

Methodologically, future studies could benefit from investigating how different levels of management intensity interact with climate impacts, offering a clearer picture of their combined effects. Additionally, incorporating more detailed data on the climatic water balance – specifically, the relationship between precipitation, evapotranspiration, and soil moisture – would strengthen the evidence for the role of water availability in vegetation shifts.

5.7 Ecological and practical implications

The changes observed in the Steigerwald have significant implications for forest management and biodiversity conservation. The decline of the herb layer reduces habitat availability for forest floor species, potentially diminishing overall forest diversity.

Managing the balance between creating canopy openings to support natural regeneration and minimizing soil drying is a key challenge. While denser forests experience higher transpiration due to more foliage, open forests expose the soil to greater evaporation through increased solar radiation. As Wachtveitl et al. (2024) note, thinning can therefore exacerbate soil dryness.

Although improved light conditions from selective thinning support regeneration, they also heighten the risk of soil moisture loss – a concern that becomes critical with rising temperatures and more frequent droughts. Prolonged dry periods further threaten the natural regeneration of tree species, complicating management efforts.

These findings highlight the need for adaptive strategies that account for both light management and soil water retention. Close monitoring and flexible approaches will be essential to ensure forest resilience. The Steigerwald exemplifies the importance of integrating targeted interventions with a broader response to climatic challenges.

5.8 Future research directions

A dense network of systematically distributed monitoring plots, reassessed at regular intervals, is essential to capture biodiversity and ecosystem changes across Germany's forests. To ensure statistically robust results, the network must encompass a large sample size, providing the necessary data to detect significant patterns and trends. In addition to vegetation dynamics, such a network should include zoological surveys to monitor shifts in animal populations, their interactions with vegetation, and their roles in ecosystem functions. This comprehensive dataset would allow the study of how forest management practices influence biodiversity, including the interplay between canopy dynamics, forest floor vegetation, and associated fauna. Key research areas include the effects of selective thinning on light availability, soil moisture, and habitat structure, which impact both plant and animal communities. By linking these insights to management practices, we can develop adaptive strategies that enhance forest resilience under changing climatic conditions while maintaining ecological integrity.

While close-to-nature management practices, such as selective harvesting and natural regeneration, have been consistently applied, their impact on the understory appears limited compared to the dominant effects of climate change. Drought and heatwaves are reshaping forest dynamics, highlighting the need for adaptive strategies that directly address the increasing environmental pressures.

Finally, it would be valuable to examine how changes in vegetation, particularly in the herb layer, affect the insects and other animals that rely on this vegetation for habitat and food, providing a more complete ecological understanding.

6 Conclusions

This study reveals significant changes in the Steigerwald forest floor vegetation, including a marked decline in herb layer cover and shifts towards greater homogeneity and altered species composition. The results emphasize the predominant influence of climate change on forest floor vegetation. Rising temperatures, fewer frost days, and persistent soil dryness have significantly altered forest dynamics, surpassing the effects of traditional forest management practices. While close-to-nature approaches like selective harvesting and natural regeneration have been consistently applied, their impact on understory vegetation is limited in comparison to the pervasive influence of climatic stressors. This highlights the urgent need to adapt management strategies to address climate change more effectively, potentially by incorporating drought-tolerant species or adjusting thinning practices.The study further underscores the vulnerability of beech-dominated forests to heat and drought, corroborating projections of a gradual shift towards more drought-resilient species such as hornbeam and oak. These findings call for adaptive and innovative management approaches to enhance forest resilience under changing climatic conditions. The importance of long-term vegetation monitoring is also evident, as it provides critical insights into environmental changes and supports the refinement of management practices.

Additionally, the study aligns with projections, that a 2°C temperature increase could disrupt site-specific ecological knowledge on one-third of Bavarian territory (Fischer et al. 2019). Early signs of this disruption are evident in floristic changes, including reduced cover and shifts in species composition, which are expected to intensify in the decades to come. These results underline the necessity of broad, proactive efforts to address climate change impacts on forest biodiversity, not only in the Steigerwald but also across other temperate forests in Central Europe.

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Author contributions

Anton Fischer (AF) developed the research project, guided the project and outlined the paper. Walter Welß recorded the vegetation in 1985 and carried out the record in 2016, supported then by Annette Sauerwein-Welß. Johanna Kocak prepared the 2016-record. Barbara Michler (BM) and Hagen Fischer (HF) carried out the data analyses, created the database and organised the data input (ST 305). AF wrote the first version of the text, BM and HF and AF further optimized the text.

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Appendix/Anhang

Appendix 1/Anhang 1

Dynamic changes in species cover values

In 1985, species cover was estimated using the Braun-Blanquet scale, whereas in 2016, continuous percentage values were recorded. For comparison, Braun-Blanquet cover classes from 1985 were converted to the midpoint of their respective percentage intervals, following Ellenberg's recommendation (Ellenberg et al. 2001, p. 28).

The Braun-Blanquet scale produces a characteristically steep-left and right-skewed distribution: low cover values are very frequent, while high cover values are rare. Thus, using midpoints can lead to a slight overestimation of cover values in 1985. However, as the following analysis shows, this effect is minor and does not account for the significant observed decline in herb layer cover.

Figure 1 visualizes the frequency and transitions of Braun-Blanquet cover classes between 1985 and 2016. The 2016 continuous cover data were transformed into Braun-Blanquet categories to ensure consistency.

The frequency of the lowest cover class "+" (< 1%) increased markedly in 2016, while mid-range classes ("1" to "4") declined substantially. The highest class "5" (> 75%) remained rare in both years (with only eight occurrences). Many species with moderate cover in 1985 (e.g., class "2") were either absent or occurred at much lower cover levels ("+" or "1") in 2016. Most newly recorded species in 2016 had very low cover values. In addition, species that were already rare in 1985 frequently disappeared entirely by 2016.

These patterns demonstrate that the distributional shift toward lower cover values reflects a genuine ecological change, not a methodological artefact. The herb layer is undergoing structural erosion, characterized by declining overall cover, the loss of dominant species, and an increasing number of species occurring only sparsely or not at all.

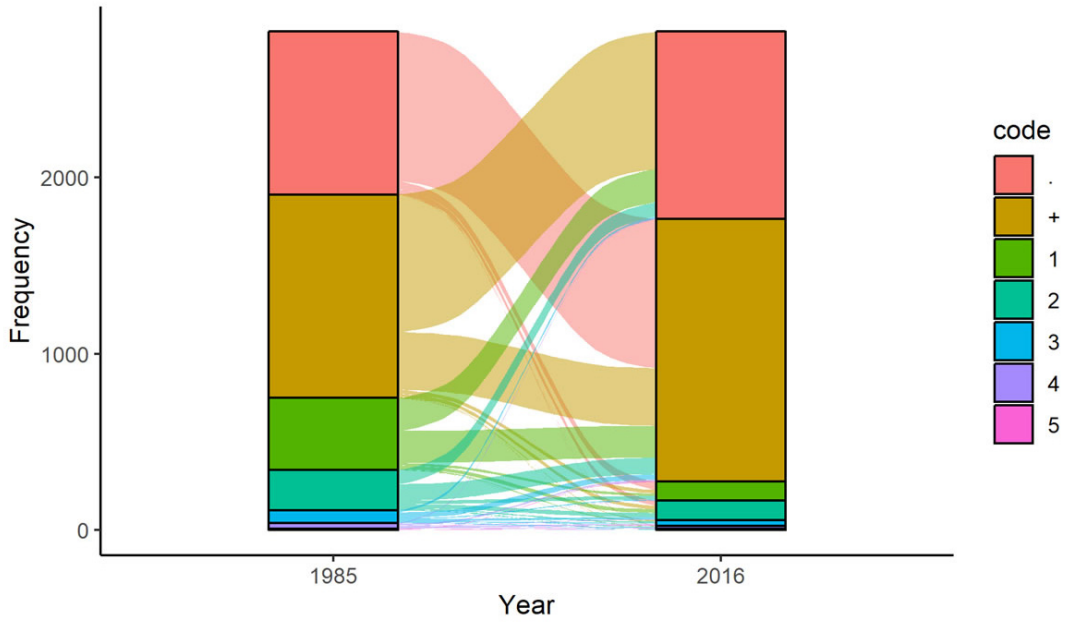


Fig. 1A: Changes in frequency and transitions of Braun-Blanquet cover classes between 1985 and 2016. Cover codes: "." = absence, "+" = < 1%, "1" = 1–5%, "2" = 6–25%, "3" = 26–50%, "4" = 51–75%, "5" = > 75%.

Abb. 1A: *Veränderungen in der Häufigkeit und Übergänge der Braun-Blanquet-Bedeckungsklassen zwischen 1985 und 2016. Deckungscodes: "." = Abwesenheit, "+" = < 1%, "1" = 1–5%, "2" = 6–25%, "3" = 26–50%, "4" = 51–75%, "5" = > 75%.*

Appendix 2/Anhang 2

Changes in species cover and frequency between 1985 and 2016

This appendix presents detailed data on species in the understory that showed significant changes in cover between 1985 and 2016. The analysis was conducted using paired Wilcoxon-test with a significance level of $p < 0.05$. The sample size consisted of 151 relevés and 286 species, with tree species recorded separately for each vegetation layer. The data include information on species cover and frequency. The species are sorted by the difference in mean cover values, from the highest positive difference (indicating an increase in cover) to the highest negative difference (indicating a decrease in cover).

Columns Explanation: Species Name, Layer: Indicates the vegetation layer the species belongs to: Overstory T: Tree layer; Understory: S: Shrub layer; H: Herb layer; M: Moss layer; F: Fern C_85 (Mean Cover 1985): The average cover value of the species in 1985; C_16 (Mean Cover 2016): The average cover value of the species in 2016; C-Diff (Difference in Mean Cover): The difference between the cover values in 2016 and 1985; F_85 (Frequency 1985): The frequency of occurrence of the species in 1985; F_16 (Frequency 2016): The frequency of occurrence of the species in 2016; F-Diff (Difference in Frequency): The difference in frequency between 2016 and 1985.

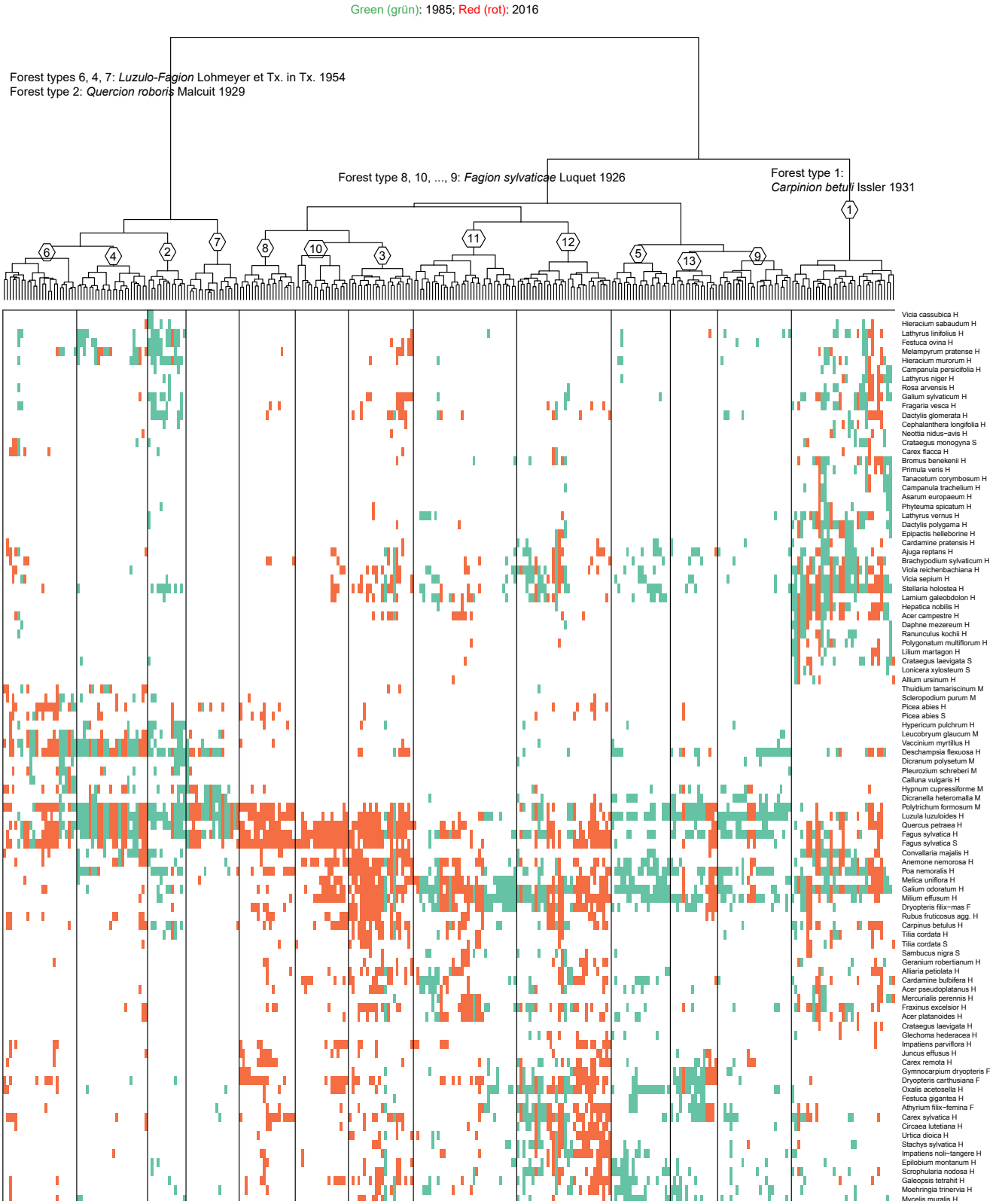
Deckung und Frequenz der Arten, deren Deckungswert sich zwischen 1985 und 2016 signifikant verändert hat; Daten Baumschicht und Unterwuchs.

Paired Wilcoxon-test $p < 0.05$; zugrundeliegender Stichprobenumfang 151 Vegetationsaufnahmen, 286 Arten (inclusive Mehrfachnennung einer Baumart in mehreren Schichten); Schichten: T = Baumschichten; S = Strauchschicht; H = Krautschicht mit Naturverjüngung; C_85: Mittelwert der Deckung der Art 1985; C_16: Mittelwert der Deckung der Art 2016; C-Diff: Unterschied im Mittelwert; F_85: Frequenz der Art 1985; F_16: Frequenz der Art 2016; F-Diff: Unterschied in der Frequenz.

Species name	Layer	C_85	C_16	C_diff	F_85	F_16	F_diff
Sorbus torminalis (L.) Crantz	T	0.000	1.000	1.000	1	22	21
Fagus sylvatica L.	S	0.855	12.461	11.606	12	108	96
Acer platanoides L.	S	0.000	0.730	0.730	0	9	9
Acer pseudoplatanus L.	S	0.000	0.564	0.564	0	11	11
Carpinus betulus L.	S	0.020	0.444	0.424	1	19	18
Tilia cordata Mill.	S	0.020	0.190	0.170	1	18	17
Picea abies (L.) H. Karst.	S	0.020	0.160	0.140	1	20	19
Fraxinus excelsior L.	S	0.000	0.134	0.134	0	7	7
Cornus sanguinea L.	S	0.003	0.000	-0.003	5	0	-5
Rubus fruticosus agg.	H	0.000	0.863	0.863	0	47	47
Impatiens parviflora DC.	H	0.000	0.744	0.744	0	33	33
Carex remota L.	H	0.065	0.192	0.127	11	27	16
Galium aparine L.	H	0.000	0.087	0.087	0	11	11
Urtica dioica L. s. l.	H	0.023	0.086	0.063	6	24	18
Rubus spec.	H	0.000	0.047	0.047	0	6	0
Carex montana L.	H	0.003	0.035	0.032	4	17	13
Anemone nemorosa L.	H	0.493	0.521	0.028	32	67	35
Rubus idaeus L.	H	0.040	0.055	0.015	3	21	18
Sorbus torminalis (L.) Crantz	H	0.001	0.014	0.013	2	14	12
Crataegus monogyna Jacq. s. l.	H	0.000	0.003	0.003	0	6	6
Pseudotsuga menziesii (Mirb.) Franco	H	0.000	0.002	0.002	0	6	6
Larix decidua Mill.	H	0.000	0.001	0.001	0	7	7
Juncus effusus L.	H	0.021	0.021	0.000	2	20	18
Tilia cordata Mill.	H	0.044	0.044	0.000	8	23	15
Solidago virgaurea L.	H	0.003	0.000	-0.003	5	0	-5
Carex umbrosa Host	H	0.006	0.001	-0.005	9	3	-6
Scrophularia nodosa L.	H	0.019	0.013	-0.006	28	19	-9
Alliaria petiolata (M. Bieb.) Cavara & Grande	H	0.164	0.158	-0.006	11	29	18
Cephalanthera damasonium (Mill.) Druce	H	0.023	0.000	-0.023	5	0	-5
Phyteuma spicatum L.	H	0.023	0.000	-0.023	6	3	-3

Senecio ovatus (P. Gaertn.. B. Mey. & Scherb.) Willd.	H	0.023	0.000	-0.023	5	0	-5
Daphne mezereum L.	H	0.025	0.000	-0.025	8	2	-6
Melica nutans L.	H	0.027	0.002	-0.025	12	3	-9
Hypericum pulchrum L.	H	0.029	0.002	-0.027	15	6	-9
Luzula pilosa (L.) Willd.	H	0.030	0.001	-0.029	16	3	-13
Festuca gigantea (L.) Vill.	H	0.048	0.001	-0.047	15	3	-12
Acer campestre L.	H	0.105	0.054	-0.051	9	27	18
Mycelis muralis (L.) Dumort.	H	0.059	0.004	-0.055	31	10	-21
Fragaria vesca L.	H	0.069	0.012	-0.057	17	13	-4
Galeopsis bifida Boenn.	H	0.063	0.000	-0.063	8	0	-8
Viola riviniana Rchb.	H	0.065	0.000	-0.065	11	1	-10
Moehringia trinervia (L.) Clairv.	H	0.077	0.005	-0.072	30	15	-15
Lathyrus linifolius (Reichard) Bässler	H	0.094	0.009	-0.085	26	7	-19
Picea abies (L.) H. Karst.	H	0.101	0.014	-0.087	4	28	24
Geranium robertianum L. s. str.	H	0.101	0.012	-0.089	4	21	17
Ajuga reptans L.	H	0.115	0.014	-0.101	28	19	-9
Calluna vulgaris (L.) Hull	H	0.104	0.001	-0.103	8	1	-7
Vicia sepium L.	H	0.140	0.019	-0.121	38	23	-15
Bromus benekenii (Lange) Trimen	H	0.127	0.004	-0.123	14	11	-3
Ranunculus auricomus agg,	H	0.125	0.001	-0.124	10	3	-7
Primula elatior (L.) Hill	H	0.160	0.014	-0.146	6	3	-3
Carpinus betulus L.	H	0.427	0.163	-0.264	20	56	36
Quercus petraea Liebl.	H	0.600	0.336	-0.264	45	97	52
Festuca ovina L. s. str.	H	0.406	0.068	-0.338	21	6	-15
Prenanthes purpurea L.	H	0.379	0.002	-0.377	10	6	-4
Cardamine pratensis L. (s. l.)	H	0.432	0.007	-0.425	14	6	-8
Galium sylvaticum L. s. str.	H	0.505	0.017	-0.488	22	17	-5
Hieracium murorum L.	H	0.618	0.018	-0.600	25	8	-17
Viola reichenbachiana Boreau	H	1.139	0.032	-1.107	31	30	-1
Poa nemoralis L.	H	2.289	1.101	-1.188	74	56	-18
Stellaria holostea L.	H	1.395	0.205	-1.190	51	31	-20
Milium effusum L.	H	3.278	2.060	-1.218	68	65	-3
Lamium galeobdolon (L.) L. s. str.	H	1.505	0.235	-1.270	29	22	-7
Oxalis acetosella L.	H	1.383	0.094	-1.289	44	29	-15
Melampyrum pratense L.	H	1.444	0.104	-1.340	20	16	-4
Cardamine bulbifera (L.) Crantz	H	1.542	0.181	-1.361	22	33	11
Calamagrostis arundinacea (L.) Roth	H	1.585	0.113	-1.472	26	19	-7
Deschampsia flexuosa (L.) Trin.	H	3.915	1.063	-2.852	65	40	-25
Vaccinium myrtillus L.	H	5.409	1.664	-3.745	31	22	-9
Galium odoratum (L.) Scop.	H	7.385	2.143	-5.242	80	80	0
Luzula luzuloides (Lam.) Dandy & Wilm.	H	6.668	0.977	-5.691	96	83	-13
Mnium hornum Hedw.	M	0.029	0.002	-0.027	15	4	-11
Dicranella heteromalla (Hedw.) Schimp.	M	0.177	0.009	-0.168	32	5	-27
Dicranum polysetum Sw.	M	0.264	0.000	-0.264	13	0	-13
Leucobryum glaucum (Hedw.) Ångstr.	M	0.346	0.022	-0.324	18	12	-6
Dryopteris carthusiana (Vill.) H. P. Fuchs	F	0.209	0.065	-0.144	22	60	38
Gymnocarpium dryopteris (L.) Newman	F	1.510	0.050	-1.460	18	18	0

Appendix 3/Anhang 3



Dynamic changes in species composition and layer cover across forest types between 1985 and 2016.

This appendix presents detailed data on species in the understory that showed significant changes in cover between 1985 and 2016 across forest types.

We focus only on significant changes in species cover within the understory for both constant and changing relevés across each of the 12 units, while also assessing significant changes in layer cover. The analysis includes tree layer 1, tree layer 2, natural regeneration in the shrub and herb layers, and the herb layer excluding tree regeneration. For understory species, when cover values were below 0.1%, frequencies were used instead. This approach highlights key patterns of change in species cover and structure, offering insights into the dynamics within stable and shifting forest types across all 13 units.

Forest type 6 (*Luzulo-Fagion*) remained largely constant, with eight constant relevés, one that left, and eight additional relevés. Within the constant group, the cover of *Deschampsia flexuosa* decreased from 7% to 1%, while *Fagus sylvatica* in the shrub layer increased from 2% to 19%, and *Vaccinium myrtillus* dropped from 41% to 11%. The overall herb layer cover declined from 67% to 21%. Among the newcomers, *Picea abies* increased in frequency from 12% to 75% in the herb layer, while *Dicranella heteromalla* decreased from 50% to 0% frequency. The cover of tree Layer 2 also increased significantly from 21% to 31%.

Forest type 4 (*Luzulo-Fagion*) had six constant pairs, while five of its relevés transitioned to Unit 8, leading to moderate shifts in species composition. Within the constant group, *Luzula luzuloides* declined in cover from 18.5% to 3%, and the overall herb layer cover decreased from 54% to 21%. In the changing group, *Luzula luzuloides* (13% to 0.04%) and *Deschampsia flexuosa* (13% to 0.1%) declined sharply, while *Fagus sylvatica* in the shrub layer increased from 2% to 23%, though it decreased in the herb layer from 2% to 0.5%. The natural regeneration in the herb layer (4% to 0.6%) also showed a significant decline.

Forest type 2 (oak forests) experienced a substantial decline, shrinking from 12 plots to just one, with only one plot remaining constant. Most plots shifted to Forest type 3 (mixed oak-beech forests) by 2016. *Anemone nemorosa* increased in frequency from 18% to 73%, and *Fraxinus excelsior* (Ash) rose from 0% to 45% in the herb layer, while the frequency of *Lathyrus linifolius* (64% to 9%) and *Leucobryum glaucum* (45% to 18%) declined. The cover of the shrub layer remained low at 2%, while the herb layer cover dropped from 53% to 18%.

Forest type 7 (Luzulo-Fagetum) retained seven constant pairs of relevés. Within these constant relevés, *Luzula luzuloides* showed a significant decline in cover from 29% to 0.3%.

Forest types 8 and 10 (*Fagion sylvaticae*) newly emerged in 2016. Forest type 8's members originated from various sources, including five plots from Unit 4 and four from Unit 9. In these newcomers, species like *Luzula luzuloides* (14% to 0.3%), *Deschampsia flexuosa* (5% to 0%), *Vaccinium myrtillus* (14% to 0.1%), and *Fagus sylvatica* (4% to 0.5%) sharply decreased in cover within the herb layer, while beech in the shrub layer increased from 1.6% to 25%. Both *Dicranum heteromalla* and *Mnium hornum* disappeared by 2016. The overall herb layer cover dropped from 44% to 6%, while natural regeneration in the shrub layer rose from 3% to 26%. Forest type 10 primarily drew relevés from Units 5, 9, and 11. The key characteristic of these relevés is beech regeneration in the shrub layer, with cover increasing from 2% to 16%. *Galium odoratum* decreased in cover from 6% to 1%, and *Dicranum heteromalla* disappeared from 33% frequency. The herb layer cover dropped from 53% to 34%.

Forest type 3 (*Fagion sylvaticae*) expanded significantly, growing from 2 relevés in 1985 to 20 in 2016, primarily by absorbing relevés from Units 5 and 2. *Fagus sylvatica* in the shrub layer increased from 0% to 10%. Species like *Rubus fruticosus agg.* increased in frequency from 0% to 65%, while *Galium odoratum* (15% to 2%) and *Stellaria holostea* (7% to 0.2%) decreased in cover. The shrub layer cover increased from 2% to 14%, while the herb layer cover nearly halved, dropping from 60% to 35%.

Forest type 11 (*Fagion sylvaticae*) decreased from 20 plots in 1985 to 15 in 2016. Seven plots remained constant, with *Melica uniflora, Milium effusum,* and *Galium odoratum* continuing to characterize the unit. Thirteen relevés shifted to Units 11, 10, 3, and 12, while eight newcomers, mostly from Units 5, 13, 9, and 1, joined Unit 11. In both the constant and changing groups, no significant changes in species cover or frequency were observed. However, in the new plots, the herb layer cover decreased from 63% to 27%, and *Mycelis muralis* dropped from 50% frequency to 0%.

Forest type 12 (*Fagion sylvaticae*) saw 7 out of 12 plots remain constant, 5 plots leave, and 13 new ones join. In the constant plots, *Galium odoratum* (9% to 1%) and *Viola reichenbachiana* (7% to 0.04%) sharply decreased in cover, and *Festuca gigantea* dropped from 57% frequency to 0%. Meanwhile, beech in the shrub layer increased from 0% to 19%, and the cover of natural regeneration in the shrub layer rose significantly from 0.03% to 20%. The overall herb layer cover decreased from 47% to 13%. In the changing group, *Carex sylvatica* declined in cover from 2% to 0.2%, while *Rubus idaeus* and *Scrophularia nodosa* dropped from 60% frequency to 0%. Among the newcomers, *Oxalis acetosella* decreased from 5% to 0.2%, while beech in the shrub layer increased from 0% to 20%. *Urtica dioica, Circaea lutetiana,* and *Geranium robertianum* increased in frequency. The total herb layer cover declined from 48% to 27%, while the shrub layer cover rose from 1% to 23%, reflecting strong natural beech regeneration.

Forest type 5 (*Fagion sylvaticae*) underwent the most significant change, completely disappearing by 2016. Originally comprising 20 relevés in 1985, none remained constant. Among the 20 changing relevés, 10 species showed significant changes. The herb layer experienced strong declines in the cover of *Galium odoratum* (13% to 1%), *Cardamine bulbifera* (4% to 0.4%), and *Oxalis acetosella* (3% to 0.4%), while *Fagus sylvatica* (0.2% to 1%) and *Quercus petraea* (0.005% to 0.5%) slightly increased. *Epilobium montanum, Scrophularia nodosa,* and *Dicranella heteromalla* decreased in frequency. Additionally, the cover of Fagus sylvatica in the shrub layer increased to 14%, while the overall herb layer cover decreased from 52% to 33%.

Forest type 13 (*Fagion sylvaticae*) experienced shifts, with seven relevés moving to Units 8 and 12. Within the constant

relevés, *Milium effusum* and *Rubus idaeus* declined from 3% cover to below detectable levels. *Mycelis muralis* completely disappeared (from 44% frequency), and *Oxalis acetosella* declined in cover from 5% to below detectable levels. Meanwhile, the cover of natural beech regeneration in the shrub layer increased from 0% to 33%, while the herb layer cover decreased from 34% to 16%. In the changing relevés, *Polytrichum formosum* declined in cover from 2% to 0.2%.

Forest type 9 (*Fagion sylvaticae*) nearly disappeared, losing 19 relevés. It was the largest unit in 1985 with 22 relevés but shrank to only three in 2016. Of these, only one plot remained constant, while two were newly formed. Among the changing relevés, seven species showed significant changes, including a drop in *Luzula luzuloides* cover from 12% to 2%. Both *Mycelis muralis* and *Dicranella heteromalla* disappeared completely. In contrast, *Anemone nemorosa* increased in frequency from 5% to 43%, and *Rubus fruticosus agg.* from 0% to 19%. The cover of natural beech regeneration in the shrub layer increased significantly from 0.1% to 11%, while it decreased in the herb layer from 3% to 0.5%. The total herb layer cover dropped from 42% to 16%, while Tree Layer 1 significantly decreased from 66% to 51%, and Tree Layer 2 significantly increased from 22% to 31%. Additionally, natural regeneration in the shrub layer rose from 0.1% to 13%.

Forest type 1 (*Carpinion betuli*), oak-hornbeam forests, remained largely stable, with 14 out of 20 relevés remaining constant. In these relevés, the herb layer cover decreased from 69% to 48%, and species like *Stellaria holostea* dropped from 6% to 0.3%. *Sorbus torminalis* increased in frequency from 0% to 36%, while *Daphne mezereum* (36% to 14%) and *Tanacetum corymbosum* (29% to 7%) showed declines in frequency. Six relevés shifted to Units 3, 11, or 12. In these changing plots, *Viola reichenbachiana* (10% to 0.1%) and *Cardamine pratense* (1.5% to 0.0%) decreased in cover, whereas *Quercus petraea* increased in frequency in the herb layer from 0% to 83%.

Appendix 4/Anhang 4

Climate data of the climate station Ebrach (located in the Steigerwald) of the German Weather Broadcast Service (Deutscher Wetterdienst, DWD).

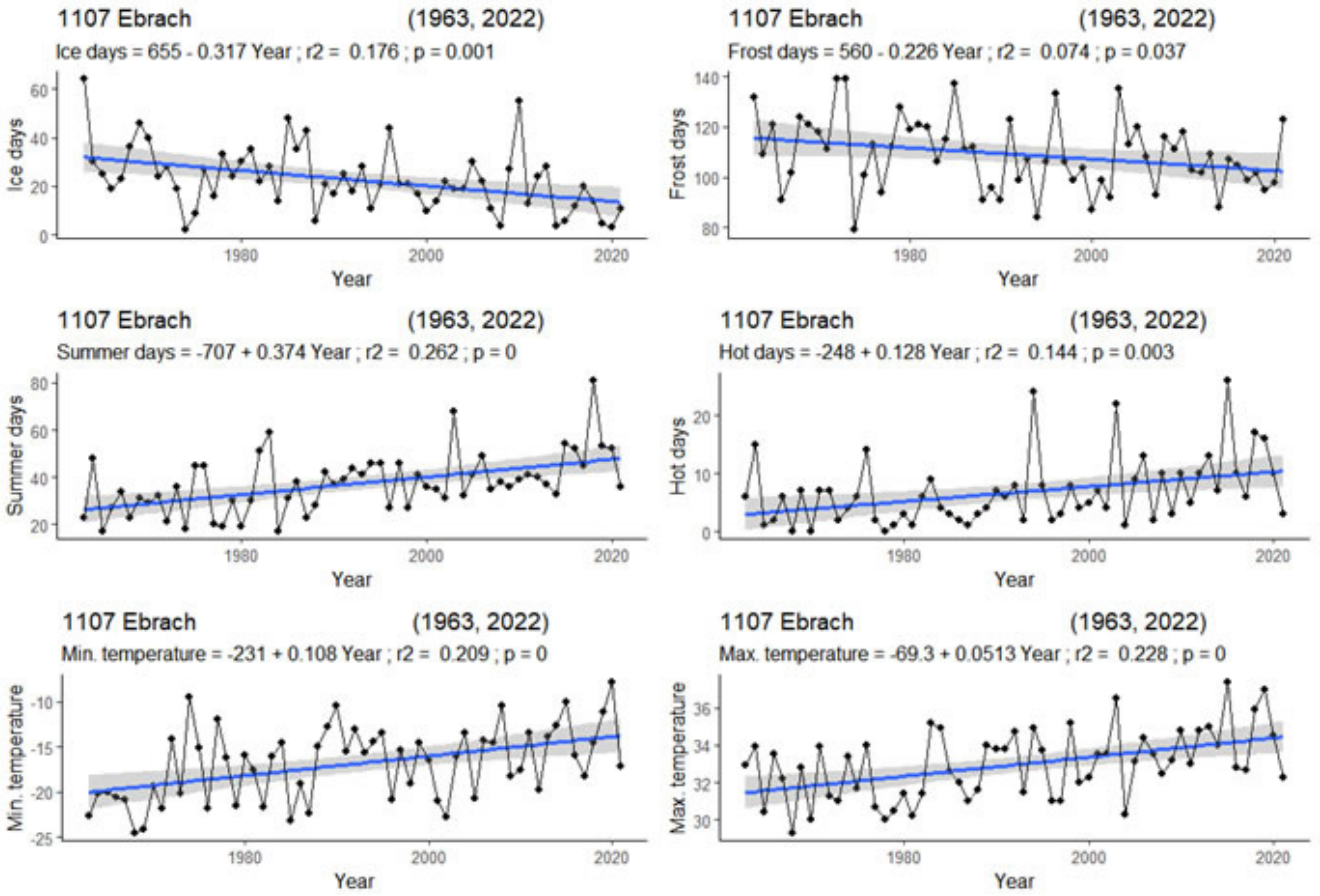


Fig. 5A: Cold days getting rarer: top left: ice days (Tmax < 0°C); top right: frost days (Tmin < 0°C). Warm days getting more frequent: middle left: hot summer days (Tmax > 25°C); middle right: very hot days (Tmax > 30°C). Extreme temperature values are changing as well. Absolute minimum is getting less cold (bottom left), absolute maximum is getting hotter (bottom right).

Abb. 5A: *Kalte Tage werden seltener: oben links: Eistage (Tmax < 0°C); oben rechts: Frosttage (Tmin < 0°C). Warme Tage werden häufiger: Mitte links: Sommertage (Tmax > 25°C); Mitte rechts: Hitzetage (Tmax > 30°C). Auch die Extremtemperaturen ändern sich: die absoluten Tiefsttemperaturen sind weniger kalt (unten links), die absoluten Höchsttemperaturen sind heißer (unten rechts).*