Universität
Bremen

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Long-term vegetation change in semi-natural grasslands – disentangling trends from pseudo-turnover

Dissertation

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Date of public disserdation defense: 08.07.2024

Title picture: View across wet meadows along the creek "Kesselherdwasser" to a hill with calcareous grassland and juniper bushes. Roßbach, Hesse, Germany, 2020.

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Thesis submitted in fulfilment of the requirements
for the degree of Doctor (Dr. rer. nat)
Faculty Biology / Chemistry
University of Bremen

Bremen, 14.05.2024

Danksagung

Ohne die Unterstützung vieler Menschen wäre es nicht möglich gewesen diese Arbeit zu schreiben. Dafür möchte ich mich hier ganz herzlich bedanken.

Mein erstes „Danke“ geht an Martin Diekmann, dafür dass du mich als Doktorandin angenommen und betreut hast. Vielen Dank für dein stets offenes Ohr, deine Unterstützung und dein Vertrauen. Danke, dass du dich auch durch wochenlanges Moose-Bestimmen nicht aus der Ruhe hast bringen lassen und mir eine große Freiheit bei der Auswahl der Themen, der Umsetzung und der Zeitplanung eingeräumt hast. Außerdem bin ich dankbar, dass du mich zu den wundervollen Menschen und Orten der IAVS und FLEUR Konferenzen mitgenommen hast. Diese Erfahrungen möchte ich nicht missen.

Als nächstes gilt mein Dank Gerald Jurasinski für die Begutachtung meiner Arbeit. Danke für dein Interesse an meiner Forschung, deine Zeit, Mühe und die Bereitschaft zu meiner Verteidigung nach Bremen zu reisen.

Ein weiterer herzlicher Dank geht an die anderen Mitglieder des Prüfungsausschusses. Vielen vielen Dank Matthew Nielsen, Christina Roggatz, Elisabeth Riedel und Verena Wutz für eure Zeit und Mühe!

Ohne die gesamte AG Vegetationsökologie & Naturschutzbiologie wäre dieses Unterfangen sehr viel trockener und mühsamer gewesen. Danke an euch, Andy, Barbara, Cecilia, Jolina, Josef, Kathrin, Martin und Tina für die gute Zeit bei Mittagessen, Boßeltouren und Weihnachtsfeiern. Schade, dass uns durch Corona so viel gemeinsame Zeit entgangen ist. Barbara und Kathrin haben die beste nur wünschbare Starthilfe geleistet. Cecilia möchte ich für die Herzlichkeit und die guten Gespräche über die Wissenschaftswelt und das Leben danken. Danke Andy, für die Analyse meiner vielen Bodenproben und dass du mich bei Diskussionen und Entscheidungen über Methodik und Bodenchemie mitgenommen hast. Ich habe sehr viel gelernt! Jolina, ich freue mich sehr, dass wir uns kennenlernen durften; mit dir zusammen haben Lehre und Feldarbeit viel mehr Spaß gemacht. Danke für das Teilen von frustrierenden und aufregenden Momenten und die Unterstützung in katastrophalen Situationen fern von Zuhause. Der erweiterte Kreis der FB2 Doktorand*innen rund um den „Science Chat“ hat den Uni-Alltag lebhafter gemacht; ich freue mich sehr, dass wir uns über die AGs hinweg zusammengetan haben.

Cord gilt mein großer Dank für das Aufmerksam machen auf die Stelle und natürlich die Einführung in die Welt der Wiederholungsstudien und der Vegetationskunde überhaupt.

Danke für deine Hilfe beim mühsamen Schreiben des ersten Manuskripts und deine Bereitschaft zu stets produktiven Diskussionen.

Bei Martin Scharpenberg vom Kompetenzzentrum für Klinische Studien Bremen möchte mich ich herzlich für die kompetente Beratung in statistischen Fragen und die Inspiration für das Hinterfragen von Methoden bedanken.

Ohne historische Daten sind Wiederholungsstudien nicht möglich, daher ein großes Dankeschön an Gerhard Ludwig, Cecilia und Martin für das Teilen ihrer Vegetationsaufnahmen.

Allen, die Teile dieser Arbeit Korrektur gelesen haben, danke ich für eure Zeit und eure sehr hilfreichen Kommentare; danke Aline, Daniel, Jolina, Manu und Martin!

Meiner WG und Freunden möchte ich danken für das warme Zuhause, eure Gesellschaft, das Interesse an meiner Arbeit, fachliche Diskussionen und für die viele gemeinsame Zeit im Home Office.

Es dauert am Ende immer länger als man denkt. Dem liebsten Grund dafür möchte ich ganz besonders danken; Lana, danke, dass du dich mitten rein gedrängelt hast und mein Leben immer wieder reicher machst. Vielen Dank Manu, dass du mir dafür vor allem in der langen Endphase so viel Raum verschafft hast.

Contents

Summary

Grasslands cover a significant part of the Earth's surface and support a large proportion of its biodiversity. Despite their importance, species-rich grasslands have been severely decimated and degraded over the past century. In Europe, grasslands are largely created by human management. At the same time, anthropogenic influences pose the greatest threat to grassland biodiversity today, due to changed land use practises. However, the continuous management also presents an opportunity to exert a direct positive influence. Resurvey studies can provide the necessary knowledge of current developments in grasslands to enable effective action. With the increasing availability of systematically recorded historical data sets, many insightful resurveys have been conducted in recent decades. However, grassland ecosystems have been under-represented in these studies.

Data collected during fieldwork often contains a significant amount of noise that may obstruct the signal that is meant to be observed. With this thesis, we aim to contribute to disentangling signal from noise in resurvey studies by introducing a metric for stochastic fluctuations in species composition and giving recommendations for dealing with a frequently problematic statistical phenomenon. Additionally, two specific resurvey studies in *Nardus* grasslands and calcareous grasslands were conducted to contribute to the growing body of knowledge on changes in grassland biodiversity.

The resurvey of *Nardus* grasslands in western Germany was carried out in 2018, 32 years after the first survey. During this period, continuous management by annual mowing took place. Our results confirmed the trend of soil pH increase in acidic soils previously observed in other Germany regions and the UK. However, the widespread eutrophication of *Nardus* grasslands was only weakly pronounced. We believe that this is due to the exceptionally consistent management of annual mowing over the previous 30 years, which has not been carried out in this form in other regions. It was able to stop or at least slow down the eutrophication processes triggered by pH recovery and atmospheric deposition. It is important to note that the timing of mowing is crucial. It should not be carried out too late in the year in order to remove a sufficient amount of nutrients.

In 2019, 11 years after the initial survey, we conducted a resurvey study of calcareous grasslands in Lower Saxony, Germany. The focus was on the effects of extreme drought on the vegetation, as these years were exceptionally dry. Due to climate change, droughts are expected to intensify in the future. However, the impact of more extreme droughts on calcareous grasslands remains unclear. The initial survey confirmed that particularly warm and dry microclimates, have had a positive effect on the characteristic species in the past. In the resurvey, the vegetation showed clear signs of the severe drought. This contradicts experimental studies that have observed the species composition of calcareous grasslands to be resilient to drought. The response to the drought varied between sites with different microclimates. Some general effects were amplified on steep, south-facing slopes, including a decrease in characteristic species. This can be interpreted as a warning that, under the influence of ongoing climate change, sites that previously favoured typical calcareous grassland species may develop conditions that are too extreme in the future.

In the methodological part of this thesis, we introduced the concept of “baseline turnover” as a measure of the extent of vegetation changes that occur regularly due to stochastic fluctuations in species composition. For this purpose, 57 time series of permanent plots in nine vegetation types worldwide were collected. The observed baseline turnover levels corresponded to commonly reported values of methodological pseudo-turnover (e.g. observer error or relocation error). It is therefore an important factor to consider when attempting to distinguish signal from noise in studies of vegetation change. Baseline turnover differed significantly between vegetation types. The main factors driving baseline turnover were plot size, saturation with species from the community pool, mean annual temperature, and the life span of the species present. As smaller plots were found to lead to higher stochasticity in observed community composition, we recommended that researchers avoid using small sampling units in studies of vegetation dynamics.

With an article on the statistical phenomenon of “regression to the mean”, we aimed to raise awareness of this potential pitfall in the statistical analysis of resurveys and longitudinal experiments. It manifests itself in a negative correlation between the change scores and the initially measured values of the same variable. This is an artefact of measurement inaccuracies in the data. In other fields, particularly medicine, the issue of regression to the mean is frequently discussed. To minimise the risk of regression to the mean distorting study results, studies should be carefully designed so that the initial sampling does not introduce a built-in bias. We also recommended that the initial values of a variable should always be included as an additional predictor when calculating models of change scores.

Uncertainties in the analysis of resurvey studies may arise from methodological inaccuracies in the data collection, inappropriate study design, and random variation in species composition. This includes relocation error and observer error, as well as the influence of non-randomly distributed sampling points on the validity of statistical tests. We conclude that it is of vital importance for the reliability of resurvey studies to recognise the problems mentioned. These aspects should be explicitly addressed in each study in order to assess the accuracy of the study and to improve the interpretation of results. Comparing observed vegetation changes to baseline turnover can help researchers assess the extent to which changes are due to random fluctuations or directional vegetation change.

Zusammenfassung

Grünland bedeckt einen erheblichen Anteil der Erdoberfläche und leistet einen großen Beitrag zur Biodiversität des Planeten. Trotz seiner hohen Bedeutung wurde es im letzten Jahrhundert stark dezimiert und degradiert. In Europa wird Grünland weitgehend durch menschliche Bewirtschaftung erhalten. Durch veränderte Landnutzungspraktiken stellt diese heute jedoch gleichzeitig die größte Bedrohung für die biologische Vielfalt dar. Andererseits bietet die kontinuierliche Bewirtschaftung auch eine sehr direkte Möglichkeit, einen positiven Einfluss auf die Artenvielfalt auszuüben. Wiederholungsstudien können das für wirksame Maßnahmen notwendige Hintergrundwissen über aktuelle Entwicklungen im Grünland liefern. Durch die zunehmende Verfügbarkeit von systematisch erfassten historischen Datensätzen konnten in den letzten Jahrzehnten viele aussagekräftige Wiederholungsstudien durchgeführt werden. Allerdings sind Grünlandökosysteme in diesen Studien bisher unterrepräsentiert.

Im Feld gesammelte Daten enthalten oft ein erhebliches Maß an Hintergrundrauschen, das die Beobachtung eines „Signals“ erschweren kann. Mit dieser Arbeit möchten wir einen Beitrag zur Trennung von Signal und Rauschen in Wiederholungsstudien leisten, indem wir eine Metrik für stochastische Schwankungen in der Zusammensetzung von Arten einführen und Empfehlungen für den Umgang mit einem häufig problematischen statistischen Phänomen geben. Darüber hinaus wurden zwei konkrete Wiederholungsstudien durchgeführt, eine in Borstgrasrasen und eine in Kalkmagerrasen.

Die Wiederholungsstudie in Borstgrasrasen in der Eifel wurde 2018 durchgeführt, 32 Jahre nach den ersten Aufnahmen. Während dieser Zeit fand ein kontinuierliches Management durch jährliche Mahd statt. Unsere Ergebnisse bestätigten den in anderen deutschen Regionen und Großbritannien beobachteten Anstieg von Boden-pH Werten. Der weit verbreitete Trend zur Eutrophierung von Borstgrasrasen war hier jedoch nur schwach ausgeprägt. Dies ist wahrscheinlich eine Folge der außergewöhnlich konsequenten jährlichen Mahd über die vorhergegangenen 30 Jahre, die so in keiner anderen Region durchgeführt wurde. Eutrophierungs-Prozesse, die durch den pH Anstieg und atmosphärische Depositionen von Nährstoffen ausgelöst werden, konnten eingedämmt werden. Ein entscheidender Faktor ist hier der Zeitpunkt der Mahd, der nicht zu spät im Jahr liegen sollte, um genügend Nährstoffe entnehmen zu können.

Im Jahr 2019, 11 Jahre nach der Ersterfassung, führten wir eine Wiederholungsstudie von Kalkmagerrasen in Niedersachsen durch. Diese Jahre waren außergewöhnlich trocken, daher lag der Schwerpunkt dieser Untersuchung auf der Reaktion der Vegetation auf die extreme Trockenheit. Aufgrund des Klimawandels werden Dürreperioden in Zukunft wahrscheinlich häufiger und stärker auftreten. Die Auswirkungen dessen auf Kalkmagerrasen sind allerdings noch unklar. Die Ergebnisse der Ersterfassung bestätigten, dass ein besonders warmes und trockenes Mikroklima, wie es auf Südhängen zu finden ist, in der Vergangenheit einen positiven Effekt auf die typischen Arten der Kalkmagerrasen hatte. In der Wiederholungsstudie zeigte die Vegetation deutliche Anzeichen der vorhergegangenen Trockenheit. Dieses Ergebnis steht im Widerspruch zu bisherigen Experimenten, in denen die Artenzusammensetzung von Kalkmagerrasen gegenüber Trockenperioden stabil war. Die Auswirkungen der außergewöhnlichen Dürre unterschieden sich je nach lokalem Mikroklima. Einige generelle Effekte waren auf steilen Südhängen besonders stark ausgeprägt, darunter auch ein Rückgang von Charakterarten der Kalkmagerrasen. Daher könnten Standorte, die bisher günstig für typische Kalkmagerrasen-Arten waren, in der Zukunft möglicherweise für diese zu extreme Bedingungen aufweisen.

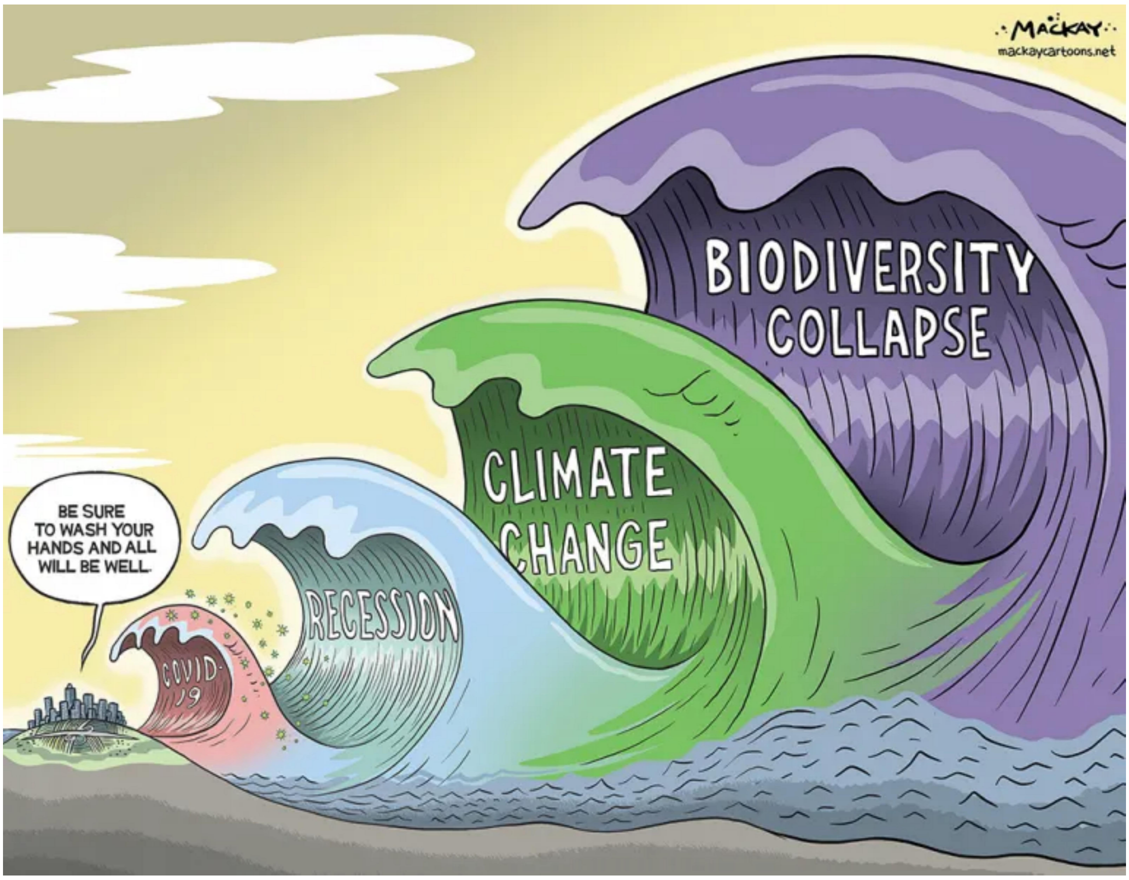
In dem methodischen Teil der Arbeit wurde mit dem Konzept „baseline turnover“ ein Maß eingeführt, das die Größenordnung von regelmäßig auftretenden zufälligen Schwankungen in Artenzusammensetzungen misst. Dafür wurden 57 Zeitreihen von permanenten Vegetationsplots in neun Vegetationstypen weltweit zusammengetragen. Werte für baseline turnover reichten teilweise an die Größenordnung von methodischem pseudo-turnover (z.B. Beobachterfehler oder Relokalisationsfehler) heran. Es kann daher relevant zum Hintergrundrauschen in Daten zu Vegetationsveränderungen beitragen. Werte für baseline turnover unterschieden sich signifikant zwischen den Vegetationstypen. Die wichtigsten Faktoren, die baseline turnover beeinflussten, waren die Größe der Plots, die Sättigung mit Arten aus der Umgebung, die mittlere Jahrestemperatur und die Lebensform der vorherrschenden Arten. Da kleinere Plots zu mehr zufälligen Schwankungen in der Artenzusammensetzung führten, ist die Empfehlung, kleine Probeeinheiten in der Untersuchung von Vegetationsdynamiken zu vermeiden.

Mit einem Artikel über „Regression zur Mitte“ möchten wir Aufmerksamkeit für dieses potentielle Problem in der statistischen Analyse von Wiederholungsstudien und Längsschnitt-Experimenten wecken. Es zeigt sich in einer negativen Korrelation der Veränderung einer Variable zwischen zwei Untersuchungszeitpunkten und dem Ausgangswert derselben Variable. Dies ist ein Artefakt von Messungenauigkeiten in den Daten. In anderen Wissenschaften, vor allem in der Medizin, ist dieser Effekt gut dokumentiert. Um das Risiko zu minimieren, dass die „Regression zur Mitte“ Ergebnisse verfälscht, sollte beim Design von Studien darauf geachtet werden, dass dieses keine inhärenten Verzerrungen produziert. Bei Modellen, die die Veränderung einer Variable durch einen Umweltfaktor erklären, geben wir die Empfehlung, dass der Ausgangswert dieser abhängigen Variable ebenfalls als erklärende Variable eingefügt werden sollte.

Unsicherheiten in der Analyse von Wiederholungsstudien können durch Ungenauigkeiten während der Datenerhebung, unangemessenes Studiendesign und zufällige Fluktuationen in der Artenzusammensetzung entstehen, Dabei sind Relokalisations- und Beobachterfehler, und der Einfluss einer nicht-zufälligen Verteilung von Probenahmepunkten auf die Aussagekraft von statistischen Tests, signifikante Faktoren. Wir kommen zu dem Schluss, dass es für die Zuverlässigkeit von Wiederholungsstudien von entscheidender Bedeutung ist, die genannten Probleme bewusst zu betrachten. Diese Aspekte sollten in jeder Studie explizit angesprochen werden, um dadurch eine Einschätzung der Genauigkeit der Studie und eine sichere Interpretation der Ergebnisse zu ermöglichen. Durch den Vergleich von beobachteten Vegetationsveränderungen mit „baseline turnover“, kann ermittelt werden zu welchem Umfang diese auf Zufallsschwankungen oder gerichteten Trends beruhen.

— Chapter 1 —

Introduction



1.1 General introduction

Among the multiple crises raging on Earth today, the biodiversity crisis is probably the most dire and simultaneously overlooked. Human societies rely heavily on ecosystems and their biodiversity for ecosystem services (Rockström et al. 2023), however increasing evidence suggests that we have entered a new mass extinction event comparable to the five big historic events in Earth's history. The global rate of species extinction is currently estimated to be hundreds to thousands of times higher than the average over the last ten million years (Barnosky et al. 2011; IPBES 2019; Cowie et al. 2022).

Grasslands harbour a large proportion of the planet's biodiversity, with their maximum plant species richness at smaller scales (< 50 m^2) even exceeding that of tropical forests (Wilson et al. 2012). About 40 % of the Earth's land mass is covered by grassland, in Europe it is approx. 35 % and in Germany approx. 14 % (Dengler et al. 2014; Dengler et al. 2020; Destatis 2021). Leuschner & Ellenberg (2017b) estimate that about 33 % of the native vascular plants of Central Europe are mainly found in grassland, Schoof et al. (2019b) place this value for Germany at more than 50 %. Grasslands are also a habitat for many specialised animal species, such as meadow birds (29 % in Europe associated to grassland, Nagy 2009) and insects (Öckinger & Smith 2007; WallisDeVries & Van Swaay 2009). Of the more than 45,000 animal species in Germany, 70 to 80 % are dependent on open habitats, with most of them being tied to extensively used grassland types (Schoof et al. 2019a). Ecosystem services of grasslands include the production of forage crops, the storage of water and carbon, the purification of drinking water, protection against soil erosion and floods, and the provision of (potential) pharmaceuticals (Schoof et al. 2019a). Furthermore, grasslands have a significant importance as cultural heritage with their high aesthetic value, which is important for tourism, but also for the personal identification with the landscape (Lindborg et al. 2023).

Despite the importance of species-rich grasslands, they have been severely decimated and degraded over the last ca. 100 years (Leuschner & Ellenberg 2017b). Globally, the share of grassland in a degraded state is estimated to amount to approx. 49 % (Bardgett et al. 2021). In the UK lowlands, around 90 % of semi-natural grasslands have disappeared since World War II (Bullock et al. 2011). In Germany, about 40 % of the area still covered by grasslands in the 1950s/1960s was converted to other types of land use until 2015 (Gömann & Weingarten 2018; BMEL 2022). Local examples can even be more extreme, with more than 70 % of the area of calcareous grasslands (a particularly species-rich and low-productive type of grassland) in the Swabian Alb having disappeared since 1900 (Poschlod & WallisDeVries 2002). Ridding et al. (2020) place the phase of the biggest losses already in the decades from 1950 to 1980. However, this only means that the destruction of grassland in terms of area has since then slowed down. The qualitative loss of biological and structural diversity continues unabated (BfN 2017). As a consequence, 44 % of all plant species occurring on grassland in Germany are endangered or have already disappeared (UBA 2018). Reasons for this lie both in the abandonment of less productive sites and the intensification of agricultural use where it was profitable (WallisDeVries et al. 2002, Dengler et al. 2014).

But how do we know about all these statistics? The monitoring of species and of our environment is an existential part of conservation ecology. A well suited method to gain knowledge about long-term changes in land use and species' occurrences are resurvey studies (Hédl et al. 2017). They comprise an initial study of vegetation in a certain place and a follow-up study in the same place, typically some decades later, to detect changes in species composition, soil chemistry, and land use. Insights from resurvey studies can often be directly exported to conservation practise. Resurveys have gained popularity over the last decades (Hédl et al. 2017), but the majority of these studies have been confined to forests (Google Scholar search "resurvey" OR "re-survey" AND forest: 13,700 results vs. "resurvey" OR "re-survey" AND grassland: 3,950 results, as of 15 March 2024). As semi-natural habitats, grasslands are heavily exposed to the influence of human activities. Resurveys provide insights into the long-term effects of anthropogenic influence and therefore offer an opportunity to adjust these land use practises with regard to biodiversity conservation based on their findings. Adapting current management practices may become increasingly important in light of ongoing climate change. As a consequence, there is an increased need for monitoring of long-term developments in grassland.

Methodological pitfalls in the conduct of resurveys have been identified, such as difficulties in pinpointing the original location, uncertainties in species identification and the impact of seasonal differences (Kapfer et al. 2017). In 2018, Verheyen et al. (2018) stated that the accuracy of resurveys is still largely unknown. The statistical analysis of resurvey studies can also present difficulties in producing robust results. To identify the driving forces behind changes in grassland with certainty, it is essential to continuously improve the corresponding analytical methods. In order to be able to estimate the accuracy of resurvey studies, the potential pitfalls mentioned above should be addressed in each resurvey. This thesis aims to contribute to the growing body of knowledge on changes in grassland biodiversity by conducting resurvey studies and reflecting on their methodology.

1.2 A (eurocentric) history of grasslands

After the last glacial period in Europe – the Weichsel/Würm glaciation – ended approximately 12,000 years ago, the glaciers and cold-steppe vegetation retreated and made way for a recolonisation of the continent by pioneer tree species. It is generally assumed that Europe was almost entirely covered by dense forests during the Subboreal (5,000–6,000 years ago), which are also considered to be the "potential natural vegetation" or climax vegetation in most parts of the continent today. Apart from azonal sites there was probably no relevant grassland flora in Central Europe at that time. These consist of salt marshes, i.e. tidally influenced grasslands on the North Sea coast, avalanche paths, and alpine grasslands above the tree line where natural conditions do not allow tree establishment (Leuschner & Ellenberg 2017a). Hejcman et al. (2013) add to this list fragmentary steppe grasslands, especially on south-facing, dry slopes, and alluvial grasslands along rivers, where the forces of water and the influence of beavers and herbivores may have prevented closed forests. This makes grasslands as we know them a vegetation type entirely dependent on human disturbance to prevent the re-colonisation with woody species. Therefore, they are often called "semi-natural" (Leuschner & Ellenberg 2017b). While this is true in the current landscape, other landscape architects than humans were present in the post-glacial landscape that are now extinct, like forest elephants, giant deer, aurochs, wild horses, and wisents. The "megaherbivore theory" suggests that the influence of those large grazing animal herds was strong enough to keep relevant areas of the landscape open and covered with grassland-like vegetation (Vera 2000; Svenning 2002). Pollen analyses from sediments of this period seem to argue against this, as pollen from open land species such as grasses are hardly detectable (Litt 2000). However, current samples from mixed forest and grassland landscapes are also difficult to distinguish from closed forests, as grazing animals are very effective at removing grasses before they flower (Vera 2000; Hejcman et al. 2013). Findings of mollusc remains from species associated with open landscapes indicate that open vegetation structures persisted in Central Europe after the end of the last ice age (Hejcman et al. 2013). The true extent to which the original megafauna was able to open up the developing forests of the Holocene is still a matter of debate. Hejcman et al. (2013) estimate the proportion of natural grasslands in Central Europe before the onset of agriculture at approximately 5 % of the total area. It seems plausible that the species-rich grassland vegetation is not only a product of human agricultural practices, but also existed as a product of natural processes.

The question of whether we have to imagine post-glacial Europe as a closed forest or as a park-like landscape with open areas (or something in between) also relates to the origin of our current grassland species. Like the tree species, they were able to invade Central and Northern Europe after the last glacial period from refugia in the Mediterranean regions and East European steppes (Frey & Lösch 2014). Important source vegetation types were floodplain- and other wet forest types as they provided enough canopy gaps for the light-demanding species (e.g. for *Deschampsia cespitosa*, *Anthriscus sylvestris*). Dry forests probably played a minor role due to their nutrient-poor soils (Dierschke & Briemle 2002). Other species probably immigrated from the meadow steppes of Southeast Europe (e.g. *Tragopogon* spec., *Crepis biennis*, Leuschner & Ellenberg 2017b).

From the Neolithic onwards, (ca. 7,500–6,800 years ago, in the Baltic and Scandinavia less than 5,000 years ago, Dengler et al. 2014) early settlements and agricultural activities led to deforestation for timber and agriculture (Dierschke & Briemle 2002; Hejcman et al. 2013; Leuschner & Ellenberg 2017a). Wood pasture, i.e. low-intensity livestock grazing in the forest, was an early and very common practice that led to the opening up of forests, making space for grass-dominated areas (Dierschke & Briemle 2002; Leuschner & Ellenberg 2017a). First evidence of hay meadows stems from the Iron Age, only ca. 2,500 years ago, when iron scythes made hay cutting possible (Hejcman et al. 2013; Leuschner & Ellenberg

2017a).

In the Roman times, large-scale forest clearings took place and hay became an important source of livestock fodder, as opposed to the earlier used tree foliage (Dierschke & Briemle 2002; Leuschner & Ellenberg 2017a). Forest cover increased again after the collapse of the Roman Empire, in the great migration period (Litt 2000), but was greatly reduced in the Middle Ages, leading to a cover of grassland of up to a third of the landscape (Dierschke & Briemle 2002; Leuschner & Ellenberg 2017a). However, a large-scale increase in hay meadows was not recorded until the 18th century, when livestock were housed in stables year-round to produce manure for the fertilisation of arable fields (Hejcman et al. 2013). Meadows with more than one cut per year are an even more modern development, as this practice is dependent on nutrient addition or irrigation.

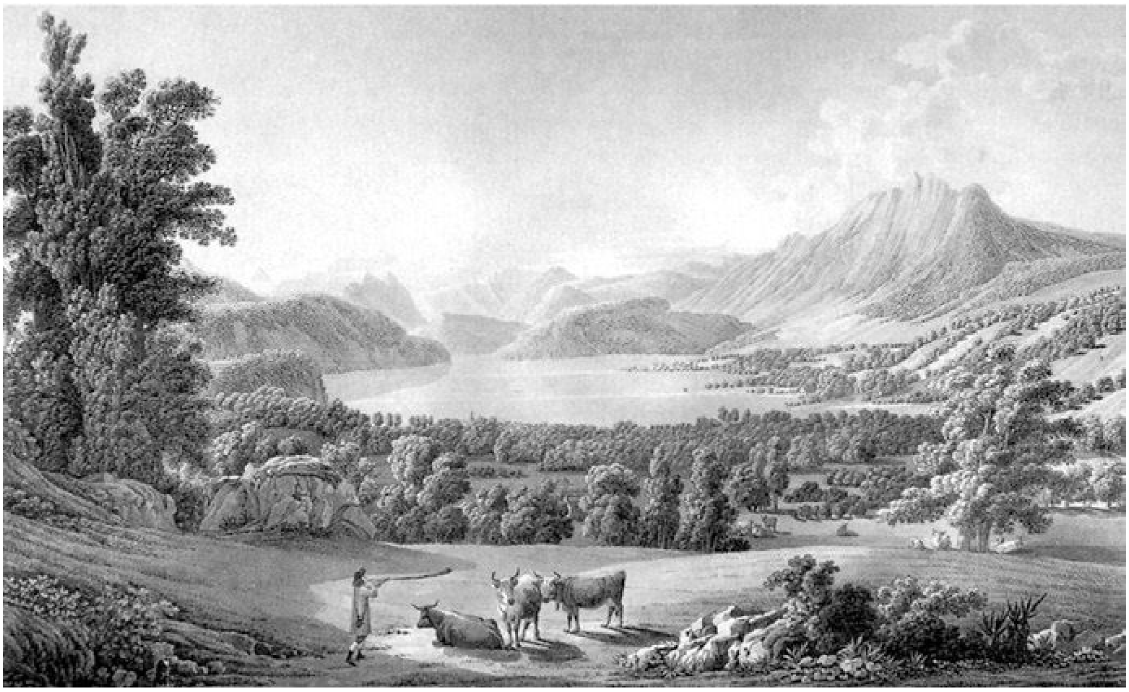


Figure 1.1: Etching of a parkland landscape north of Lake Lucerne (Switzerland), ca. 1800 by Peter Birmann (Leuschner & Ellenberg 2017a).

In the industrial age, when the demand for wood for charcoal or potash exploded, the usage of the landscape was further intensified. The soils of grasslands and heathlands were gradually depleted from nutrients in this time, either directly by sod cutting or indirectly by mowing and grazing, constantly removing biomass. Characteristic species of traditional species-rich grasslands are therefore often adapted to low-nutrient conditions, which enable the co-existence of many stress-tolerant species instead of only a few competitive ones. A romantic image of a natural landscape that often defines our ideas of nature conservation stems from this time period (Leuschner & Ellenberg 2017a). The park-like landscape that had established by the 1850s through exploitation of every corner of the landscape by wood pasture, grazing, hay making, and, where possible, agriculture, was idealised in the industrial period, when many people lived in densely populated and polluted areas (Mose & Weixlbaumer 2012). Even though these park-like landscapes were shaped by human activity, Poschlod et al. (2005) estimated that here, the diversity of plant species was the highest in history. This was due to a high small-scale structural diversity and nutrient depletion, which allowed many species to coexist in small areas. Today's species-poor, intensively used, high-yield meadows have been formed since the 1950s with the increased availability of artificial fertilisers (Frey & Lösch 2014). The development of grasslands as we know them and perceive as natural part of our environment is therefore a quite recent development. It has nonetheless been long enough to enable the formation of characteristic floras and communities (Leuschner & Ellenberg 2017a).

Many of today's conservation practices have to do with re-establishing or imitating traditional land uses in order to create historical landscape structures (which, in turn, mimic the impact of grazing mega-herbivores that shaped open structures before (Pärtel et al. 2005)). These are often tedious and, from today's perspective, expensive, which is why they were abandoned in the first place (Poschlod & WallisDeVries 2002).

1.3 Different types of semi-natural grassland

Grassland can be divided into categories by different criteria. The most obvious is the management type: grazing or mowing. Pastures are kept open by grazing, which leads to a more patchy species distribution, as the animals select which species are preferably eaten (Dierschke & Briemle 2002; Leuschner & Ellenberg 2017b). Additionally, more nutrient-rich excrement patches are formed, the distribution of which depends on the animal species (e.g. concentrated in one corner for horses, distributed over the whole pasture for cows). "Pasture weeds" are favoured especially by "undergrazing", i.e. low densities of grazing animals (Dierschke & Briemle 2002; Leuschner & Ellenberg 2017b). Theses are species that are avoided by grazers due to spikes, poisonous contents, or low nutrients, such as thistles. Additionally, the hooves of grazing animals frequently lead to open soil patches, where germination is facilitated (Leuschner & Ellenberg 2017b).

In contrast, the regular mowing of meadows gives all present plants the same starting conditions, as they are reduced to the same height at the same time point (Dierschke & Briemle 2002; Leuschner & Ellenberg 2017b). This favours fast-growing species with good regeneration capacities and makes meadows more homogeneous in structure (Leuschner & Ellenberg 2017b). Additionally, herb species that are sensitive to trampling occur here in greater numbers (Leuschner & Ellenberg 2017b). From the point of nature conservation, pastures are often preferred, as their more diverse structures are beneficial to insects and other animals (Dierschke & Briemle 2002; Dengler et al. 2014). However, low-competitive plant species often profit from a mowing regime, leading to higher total plant species numbers in mown grasslands (Dengler et al. 2014; Leuschner & Ellenberg 2017b). There are of course also mixed forms of management, e.g. grazing with one additional cut in autumn.

Another criterion used to classify grasslands is their species composition, which in turn depends on factors such as climate, soil conditions, and management. At the dry end of the spectrum are low-productive grasslands, usually divided by their soil properties into acid (*Corynephorion*) and calcareous dry grasslands (*Xerobromion*/*Mesobromion*). Fertilisation is rarely applied here as it does not improve yields due to water stress. On acid soils, *Nardus* grasslands form in less dry to moist conditions. On moist to wet soils, moor-grass meadows (*Molinion*) or marsh marigold meadows (*Calthion*) are found. At the wettest end of the spectrum are the small-sedge fens (*Caricion*). Fertilisation alters the species composition in a way that oat-grass meadows (*Arrhenaterion*) can grow in slightly dry to slightly moist conditions. These can still be species-rich at moderate levels of fertilisation. With high nutrient inputs, the grasslands are transformed into species-poor and highly productive stands (*Cynosurion*) (Leuschner & Ellenberg 2017b).

This thesis features two very different types of grassland: *Nardus* grasslands (Chapter 2) and calcareous grasslands (*Mesobromion*, Chapter 3). The following sections provide a brief characterisation.

1.3.1 Semi-arid calcareous grasslands

Calcareous grasslands grow on shallow soils formed on base-rich bedrock made of dolomite or limestone with high pH values (typically 7.1 to 8, Leuschner & Ellenberg 2017b). They are often found on south-facing slopes, which, combined with the shallow depth of the soil, creates quite extreme microclimatic conditions: hot and dry in summer and cold in winter (Leuschner & Ellenberg 2017b). Numerous species from the (south) eastern European steppes and karst landscapes, which are adapted to survive droughts and cold, have therefore been able to colonise these habitats (Leuschner & Ellenberg 2017b). The water-limited and usually low-nutrient conditions result in a low productivity (Leuschner & Ellenberg 2017b).

In Chapter 3, only semi-arid calcareous grasslands (*Mesobromion* Oberd. 1949) are considered. In the study sites located in the (sub)oceanic region of Germany, they can occur on south-facing slopes. Further south, these would be occupied by dry grasslands (*Xerobromion* Br.-Bl. et Moor 1938, Leuschner & Ellenberg 2017b).

Species richness and diversity in Europe are generally higher on calcareous than on acidic soils. The prevailing interpretation for this is that during the last ice age more calcicole than acidophilic species survived in refugial areas. These were mostly located in South European mountain ranges with abundant limestone and dolomite (Chytrý et al. 2003; Ewald 2003). A surprisingly large proportion of the total German plant species pool (approx. 15 %) is restricted to calcareous grasslands (WallisDeVries et al. 2002; Dengler et al. 2014) and they show a record-breaking plant species density on a local scale (Wilson et al. 2012). Typical species include: *Anthyllis vulneraria, Carex caryophyllea, Cirsium acaulon, Helictotrichon pubescens, Leontodon hispidus, Origanum vulgare, Pimpinella saxifraga, Plantago media, Primula veris*, and *Sanguisorba minor* (Willems 1982). The two main grass species that can

Figure 1.2: a): Landscape view of calcareous grasslands with Juniper bushes (*Juniperus communis*) near Alendorf (North Rhine-Westphalia, Germany). b): Some typical species of calcareous grasslands, from top left to bottom right: *Allium oleraceum, Primula veris, Thymus pulegioides, Ophrys insectifera, Centaurea scabiosa, Centaurium erythraea, Anthyllis vulneraria, Fragaria viridis.*

gain dominance are *Bromus erectus*, preferably in mown sites, and *Brachypodium pinnatum* which is more resistant to grazing (Leuschner & Ellenberg 2017b). Due to the occurrence of many rare and beautiful species (such as many orchids), calcareous grasslands are often in the focus of conservation planning (Poschlod & WallisDeVries 2002).

Semi-arid calcareous grasslands can be found throughout Europe from the South of France to southern Sweden and from the UK to Slovakia (Preislerová et al. 2022). Historically, the majority of semi-arid calcareous grasslands have been created in the Middle Ages by the removal of woodland, followed by extensive grazing and sometimes also hay-making, usually without any fertilisers applied (Willems 1982; Leuschner & Ellenberg 2017b). They are therefore dependent on management, as most sites would also support forest growth (Leuschner & Ellenberg 2017b). Even if they are now only found in small remnant populations, they are basically distributed throughout Germany, with the exception of the northern lowlands (BfN 2019).

Semi-arid calcareous grasslands are protected under European law as habitat No. 6210 in the Habitats Directive, prioritarily if with orchids. Their conservation status in Germany is stated as unfavourable–bad with a worsening trend (BfN 2019).

Figure 1.3: a): Wet *Nardus* grassland near Berk (North Rhine-Westphalia, Germany). b): Some typical species of *Nardus* grasslands, from top left to bottom right: *Polygala serpyllifolia, Nardus stricta, Potentilla erecta, Gentiana pneumonanthe, Arnica montana, Carex pulicaris, Pedicularis sylvatica.*

1.3.2 *Nardus* grasslands

Nardus grasslands are formed on acidic and relatively low-nutrient soils, with pH values typically ranging from 3 to 5.5 (Peppler-Lisbach & Petersen 2001, 4.1 to 5 in Leuschner & Ellenberg 2017b) and low base saturation levels of approx. 22 % (Leuschner & Ellenberg 2017b). A thick humus layer is often formed on top of the mineral soil. Due to the low pH values, acidity may fall below the threshold for aluminium toxicity (4.5, Scheffer & Schachtschabel 2010). *Nardus* grasslands are associated with a rather humid, oceanic climate with at least 550 mm of annual rainfall and only moderate differences in mean temperature between summer and winter (Peppler-Lisbach & Petersen 2001). The prevailing species are adapted to acid conditions and show a low productivity. Compared to intensive grasslands they can be recognised from afar in the landscape as yellow/brown patches (Peppler-Lisbach & Petersen 2001).

Nardus grasslands can be found throughout oceanic Europe, from Spain to Scandinavia. Historically, they covered large areas of the siliceous low mountain ranges and were used as extensive pastures or meadows on common land (Peppler-Lisbach & Petersen 2001). Today, their distribution in Germany is mainly confined to (sub-)montane areas with siliceous bedrock, and some scattered and impoverished occurrences in the northern lowlands (BfN 2019; Schwabe et al. 2019). Usually, the remaining sites are small and surrounded by other types of grassland (Peppler-Lisbach & Petersen 2001). *Nardus* grasslands are dependent on management, either extensive grazing or mowing with one cut per year, and would otherwise develop into forests (Peppler-Lisbach & Petersen 2001; Schwabe et al. 2019). There are different subtypes that can be divided either by the wetness of the soil (*Violenion caninae* Peppler-Lisbach et Petersen 2001 on fresh/moderately dry soils, *Juncenion squarrosi* Oberdorfer 1957 on wet soils) or the altitude (*Nardion strictae* Braun-Blanquet 1926 in the alps and summits of the low mountain ranges).

The species richness of *Nardus* grasslands depends on the base saturation of the soil (availability of Mg^{2+}, Ca^{2+}, K^{+} etc.) – they can be rich in flowers if the base supply is relatively good, but can also be dull and dominated by grasses (Peppler-Lisbach & Petersen 2001). With a comparable base supply, mown *Nardus* grasslands are generally richer in species than grazed formations (Peppler-Lisbach & Petersen 2001). Characteristic species include: *Antennaria dioica, Arnica montana, Carex pallescens, Carex pilulifera, Hieracium lactucella, Luzula campestris, Luzula multiflora*, and *Polygala serpyllifolia* (Peppler-Lisbach & Petersen 2001). Typical grasses are: *Nardus stricta*, accompanied by *Deschampsia flexuosa, Festuca rubra/F. nigrescens*, and *Agrostis capillaris* (Leuschner & Ellenberg 2017b). Dwarf shrubs such as *Calluna vulgaris*, *Genista anglica/pilosa*, and *Vaccinium myrtillus* are frequently found in *Nardus* grasslands, less so when mowing is the dominant management form (Peppler-Lisbach & Petersen 2001).

Species-rich *Nardus* grasslands are protected under European law as habitat No. 6230 in the Habitats Directive. Their conservation status in Germany is stated as unfavourable to bad with a worsening trend (BfN 2019).

1.4 Current changes and threats to grassland biodiversity

Species-rich grasslands of all kinds face a multitude of threats today. Many publications agree that land use changes are the biggest threat today, while climate change, atmospheric depositions, and the invasion of neophytes are subordinate factors (Sala et al. 2000; Habel et al. 2013; Török & Dengler 2018).

Land use change away from traditional agricultural practices that enabled the high biodiversity in the 19th century has intensified especially after World War II, with the widespread availability of artificial fertilisers and cheap energy (Poschlod et al. 2005). Land use change is an umbrella term that comprises several issues: quantitative losses of area can be caused by the abandonment and sometimes subsequent afforestation of marginal land, or the conversion to arable fields or even settlement area. A loss in grassland quality is often caused by "melioration", i.e. the optimisation of yield by fertilisation, drainage, and intensive use (Poschlod et al. 2005). These processes have different effects on the diversity of plant species.

1.4.1 Quantitative area losses

Abandonment or conversion to other types of land use leads to quantitative losses in area. Data of the BMEL (2022) estimate the area covered by grassland in Germany to have declined from approx. 24 % (41 % of the agricultural area) in the 1950s/1960s to approx. 14 % (28 % of the agricultural area) in 2015 (Gömann & Weingarten 2018). In recent decades, this trend has slowed down and only two percentage points have been lost since 1995/1996 (BMEL 2022). However, a survey of agricultural authorities has shown that they expect a further loss of farmers capable of practising extensive forms of grassland use in the near future in 70 % of jurisdictions. The area of high-quality grassland still existing today is therefore acutely threatened by (further) abandonment and change of management (Schoof et al. 2019a). As a consequence of this decline, grassland areas are increasingly fragmented, meaning patches are smaller and less well-connected. Following the metacommunity theory (Leibold et al. 2004), biodiversity should be greater in larger grassland patches that are better connected, which was confirmed by studies from e.g. Belgium, Estonia, and Austria (Adriaens et al. 2006; Helm et al. 2006; Zulka et al. 2014). Plants in larger patches experience less edge effects, where the conditions in neighbouring areas influence those in the grassland (Krause 2014). They can additionally support larger and more genetically diverse populations, with less fluctuations in population size and a lower probability of random extinction events. A good connection between grasslands facilitates gene flow, which can increase local diversity by allowing species to spread across the landscape (Pärtel et al. 2005). Isolation and declining population sizes can lead to genetic depletion, resulting in reduced fitness in terms of germination, survival, and fecundity (Poschlod & Schumacher 1998).

The connectivity between grassland patches is not only determined by their distance, but also by the availability of dispersal vectors. Especially since many grassland specialists have short dispersal ranges (Krause 2014), animal herds such as sheep have historically been an important vector for seed dispersal (Pärtel et al. 2005; Leuschner & Ellenberg 2017b). The fleece of a single sheep has been found to contain up to 8,500 diaspores of 85 species (Fischer et al. 1996). Until the 19th century, transhumance was a common practise, with distances between summer and winter pastures amounting up to several hundred kilometres (Poschlod & WallisDeVries 2002). With all these effects combined, habitat fragmentation is one major reason for the loss of biodiversity in grassland habitats.

1.4.2 Qualitative losses

In addition to the loss of area, land use change contributes to the qualitative deterioration of stands. Fertiliser input, intensive usage, and drainage have led to an impoverishment of the species communities, so that in Germany, only 15–20 % of grasslands were considered relatively species-rich ($>$ 20 species per 10 m^2) in 2012. Today, the biggest share of species-rich grasslands can be found in the low mountain ranges and the Alps (Schumacher 2013).

Fertiliser input has increased drastically since the 1950s (Leuschner & Ellenberg 2017b).

Figure 1.4: Intensively (background) and less intensively (foreground) used grassland near Harpstedt (Lower Saxony). The meadow in the background is regularly ploughed and re-sown with *Lolium multiflorum* as single grass species.

Nitrogen is a key nutrient for optimising yields (Dierschke & Briemle 2002) and used to be reserved for arable fields. Until the middle of the 20th century, grasslands were traditionally only fertilised with phosphorous or sodium, sometimes with manure (Poschlod & Schumacher 1998). Today, nitrogen applications of more than 150 kg N ha^{-1} a^{-1} are common (Poschlod & Schumacher 1998; Schumacher 2013). However, Schumacher et al. (2007) estimate that species-rich grassland can only be maintained at rates below 50 kg N ha^{-1} a^{-1}. As fertilisation enables higher productivity, fast-growing species that are able to quickly react to increased nutrient availability outcompete subordinate species adapted to nutrient-poor environments (Bobbink et al. 1998; Roem & Berendse 2000; De Graaf et al. 2009). As a consequence, intensively used grasslands may be so impoverished that they are composed nearly exclusively by nutrient demanding generalists with 5–10 species per 10 m^2 (Schumacher 2013). The increased productivity enables farmers to make earlier and more frequent cuts in meadows, harvesting more biomass in the process. While under an extensive management, one to two cuts per year, mostly between June and August, were common, today's intensively managed meadows are cut more than four times a year, starting as early as in the end of April (Dierschke & Briemle 2002). This frequent cutting hinders the plants from completing their growth cycles so that they cannot flower or fruit before the next cut (Zechmeister et al. 2003). Species that are dependent on reproduction by seeds are therefore decimated or excluded.

To facilitate an early trafficability of sites, drainage is often applied especially in wet grasslands (Dierschke & Briemle 2002). Those are most common in low-lying areas such as northern Germany. As a result, wet grassland specialist species have almost completely disappeared in the North German lowlands (Diekmann et al. 2019). Drainage eliminates the environmental conditions to which wet meadows plants like *Silene flos-cuculi* or *Caltha* *palustris* are adapted and leads to their disappearance (Leuschner & Ellenberg 2017b). In addition, it typically increases carbon (C) and nitrogen (N) mineralisation, resulting in an additional eutrophication of grasslands (Krause et al. 2011). Drainage and the associated increase in soil aeration can also lead to acidification of grassland, by promoting processes such as nitrification and iron sulphide oxidation (Leuschner & Ellenberg 2017b). The main winners are again nutrient-demanding generalist species, here especially the tall and fast-growing *Alopecurus pratensis*, which tolerates frequent mowing better than many other grassland plants (Leuschner & Ellenberg 2017b).

As the discussed practises are applied similarly in the whole landscape, their effects may lead to a homogenisation of grassland vegetation (Gossner et al. 2016). Natural differences between sites are being levelled out, leading to increasingly similar species compositions in more and more areas.

The opposite of intensification is grassland abandonment and subsequent fallow. When the regular removal of biomass by mowing or grazing ceases, species that can become dominant if left undisturbed gradually increase in abundance (Dierschke & Briemle 2002). At first, this may be competitive grasses or tall herbs such as *Brachypodium pinnatum, Molinia caerulea, Astragalus glycyphyllos, Solidago virgaurea*, and *Heracleum sphondylium*, depending on the type of grassland (Peppler-Lisbach & Petersen 2001; Leuschner & Ellenberg 2017b). The light-adapted grassland species are then outcompeted, resulting in a decline in species richness, particularly affecting small-sized species (Pykälä et al. 2005; Leuschner & Ellenberg 2017b). In addition, stands often show signs of eutrophication due to optimised internal nutrient cycling. Without removal of their above-ground biomass, the plants are now able to transfer nutrients into the roots before winter (Leuschner & Ellenberg 2017b). This process is also known as "auto-eutrophication" (Dierschke & Briemle 2002). Woody species appear later, but how fast this happens is dependent on local conditions (Pykälä et al. 2005; Leuschner & Ellenberg 2017b). Tree establishment may be hindered for several decades if a thick litter layer is present, preventing the germination and establishment of seedlings (Pärtel et al. 2005; Pykälä et al. 2005). The same litter layer may also prevent the regeneration of grassland specialist populations (Pykälä et al. 2005; Leuschner & Ellenberg 2017b). On most sites, the degradation caused by abandonment leads to a complete transformation of the former grassland into scrub and then woodland over time, turning the qualitative loss into a quantitative loss.

More indirect effects on grassland biodiversity are exerted by atmospheric depositions, most notably of nitrogen (in the form of nitrate and ammonium) and sulphur oxide (Sala et al. 2000). In the course of industrialisation, sulphur oxide immissions from incineration plants increased strongly and led to acidified soils ("acid rain") throughout Europe (Leuschner & Ellenberg 2017a). An acidification of the soil leads to the leaching of nutrients and base ions until, at pH values below 4.5, toxic effects can occur due to released aluminium ions (Scheffer & Schachtschabel 2010; Leuschner & Ellenberg 2017a). Inputs of sulphur oxide from the air have decreased by over 90 % across Germany since the 1990s due to effective regulations.

This was mainly achieved through the installation of filters on incinerators and the declining use of lignite (UBA 2019). Since the mid-2000s, first signs of a recovery of soil pH values and vegetation as a result of decreasing sulphur oxide depositions have been found (Rose et al. 2016; Mitchell et al. 2017; Peppler-Lisbach & Könitz 2017).

Depositions of nitrogen in reduced (NH_x) and oxidised form (NO_x) are today on average 4–20 times above the natural level (Leuschner & Ellenberg 2017a). While NO_x emissions, whose main sources are exhaust gases from industry and traffic (UBA 2014), have been reduced by more than 40 % in Germany since 1995, NH_x emissions have increased by 12 % in the last 20 years (UBA 2018). This is mainly due to the intensification of agriculture, which is the main source of NH_x emissions (UBA 2014). Nitrogen emissions have an eutrophying effect, but can also contribute to soil acidification through the nitrification of ammonium (Stevens et al. 2011).

Depending on the type of grassland, nitrogen and sulphur oxide depositions can have different effects. Acidification by sulphur or ammonium deposition plays a negligible role for grassland on soils with high pH values like calcareous grasslands where the deposited acids are offset by the buffer capacity of the soils. On acid soils, however, the buffer capacity is low, leading to a stronger acidification and decimation of acid-sensitive species. The eutrophying effect of nitrogen deposition, however, affects all types of grasslands, often leading to increased productivity in those species able to transfer the additional nutrients into quick growth (often grasses such as *Brachypodium pinnatum* in calcareous grasslands, Bobbink & Willems 1987). Those are then able to outcompete other species, especially low-growing forbs.

Atmospheric deposition of phosphorous plays a subordinate role, with estimated values for Europe of 0.27 kg P ha^{-1} a^{-1}. Dry deposition from agricultural soils and dust is the major contributor (Pan et al. 2021).

Climate change as a driver of weather extremes is expected to become an increasingly important factor for biodiversity (Thuiller et al. 2005; Behrens et al. 2009; Pompe et al. 2011; Metzing 2016). Modelled impacts on plant species include species range shifts and local extinctions (Thuiller et al. 2005). Although a direct causal link between single extreme weather events and anthropogenic climate change is impossible to prove, a recent review found numerous examples of detrimental effects of climate change on biodiversity (Pecl et al. 2017). A warming of 1.6 °C compared to pre-industrial times has already been observed for Germany in 2019 (Kaspar & Friedrich 2020). Behrens et al. (2009) calculated the sensitivity of plant species in West Germany to expected climatic changes. The main beneficiaries of climate warming were found to be nitrophilous ruderal species, including a striking number of neophytes. Many species of calcareous grasslands, thermophilic margins, and rock and boulder communities could also potentially benefit. However, due to the small area and strong spatial isolation of their habitats and the lack of effective dispersal vectors, these species are unlikely to expand beyond their current ranges, even if the climatic conditions would allow it. Climate change will have a particularly negative impact on warmth-averse species of the mountain ranges which have limited possibilities of an escape "upwards". These include a conspicuous number of species of mountain meadows and montane *Nardus* grasslands. Due to changes in the climatic water balance, many wetland plants growing in wet meadows are also expected to be negatively affected by climate change. The situation is particularly precarious for species with low dispersal potential and close ties to nutrient-poor sites, such as *Molinetalia* meadows. Warming may also have indirect effects via nutrient availability, as rates of mineralisation are increased at higher temperatures (Liu et al. 2017).

1.5 Resurvey studies

The idea of repeating a previous study and resampling the vegetation to uncover changes is well-established; resurvey studies were already published at least from the 1920s (e.g. Conard & Galligar 1929; Weaver & Albertson 1943). With the availability of systematically recorded historical data sets increasing in recent decades, a growing number of informative studies are being carried out using this method (Hédl et al. 2017).

Resurvey studies usually do not have a-priori hypotheses that are supposed to be tested by repeating vegetation sampling. In contrast, the idea is to explore potential long-term changes in species composition and to identify their drivers. They are also used as an indirect method to infer environmental changes that can be read from the vegetation change (Hédl et al. 2017). A disadvantage of resurvey studies is that drivers of change are often manifold and interconnected which makes it hard (but worthwhile) to identify the most important factors. Experimental studies in which environmental conditions are actively manipulated can complement them in investigating the influence of specific environmental variables on vegetation change. However, experiments are rarely conducted over longer periods of time – with notable exceptions like the Park Grass Experiment (Silvertown et al. 2006) and the Rengen Grassland Experiment (Hejcman et al. 2007) – which limits their potential. Long-time observations as performed in resurveys are therefore irreplaceable to gain valuable insights into the actual vegetation change.

The potential for resurvey studies is high, with 3,798,160 vegetation plots registered and available in the Global Index of Vegetation-Plot Databases (GIVD) by 2023 (Jansen et al. 2012). Of those, approx. 67 % (2,544,767) were sampled before the year 2000, making them potentially valuable to resample. However, data from grasslands are under-represented in this database, with only 57 databases with a total of 509,621 plots labelled with the search term "grassland", as opposed to 202 databases with 2,234,091 plots for the term "forest" (Dengler et al. 2011).

1.5.1 Methodological problems with data sampling

A notorious source of uncertainty and error in resurvey studies are biases arising from data sampling, i.e. the so-called “observer error”, “relocation error”, and “seasonal error”. They may inflate the observed change due to methodological inaccuracies. This leads to “pseudo-turnover”, an amount of random error that is added to the temporal change in vegetation (Kapfer et al. 2017). The phenomena have been identified at least since the 1940s (e.g. Hope-Simpson 1940; Smith 1944), but have gained more attention since the 1980s (Morrison 2016). Morrison (2016) recommended caution in interpreting detected changes in species composition of less than approx. 25 % as directional, i.e. non-random. Generally, pseudo-turnover is more relevant when actual changes are small (e.g. after short time periods), and less of a problem when pseudo-turnover is considerably smaller than actual turnover (Ross et al. 2010; Burg et al. 2015).

Observer error

The concept “observer error” describes the discrepancy that arises between two different observers when recording data. A distinction can be made between “intra”- and “inter”-observer bias. The former describes the unavoidable variation that occurs even when the same person repeats a plot, and the latter refers to the differences that arise between two different observers. One can differentiate between “overlooking error” (one observer notes a species and another does not) and “misidentification error” (both note the same plant as a different (sub-)species). Additionally, “estimation error” arises when cover values are estimated differently by several observers (Morrison 2016).

In a review of 59 articles that directly estimated observer error in their studies, 54 were found to display significant amounts of observer error (Morrison 2016). Mean values for inter-observer error ranged from 10 to 30 %. This means that, for example, 10 % of the species were only observed by one scientist, but not another. Values for intra-observer error averaged around 15 %. The mean overlooking error was estimated to be 10 to 30 %, while the misidentification error ranged from 5 to 10 %. Derived metrics such as diversity indices and results of multivariate analyses were also found to be sensitive to observer error. Other articles reported observer error values in comparable orders of magnitude. Futschik et al. (2020) reported 5–13 % discrepancies between two observers in alpine vegetation, Lisner & Lepš (2020) found on average 16 % in a species-rich wet meadow. The results by Milberg et al. (2008) showed much higher values with a mean of 26 % observer error in North European forests. However, this differed widely between species groups, with mosses of mesic habitats having a low value of 3 % and tall sedges of 74 % observer error. Verheyen et al. (2018) reported 15 % species richness difference in European forests. Across dry grasslands, flood plains, fens, and raised bogs, Boch et al. (2022) identified average pseudo-turnover values of 29 % when raw species lists are compared. Nonetheless, mean Ellenberg indicator values did not differ significantly here between observers. Aggregating layers, as well as subspecies to the species level and critical species to aggregates, reduced pseudo-turnover to 17 %.

A wide range of uncertainties in visual estimates of cover values was found, with the variation between observers sometimes reaching or exceeding 100 % (Morrison 2016). Rare species were more susceptible to varying cover estimates, with possible values of several hundred percent, whereas highly frequent species regularly showed variation in the range of only 25 to 50 %. When categories, such as Braun-Blanquet scores, instead of precise percentages were employed, deviations by one category were common (33–48 % of cases), while observers rarely differed by two categories (3–6 %, Morrison 2016). Futschik et al. (2020) reported an average of 60 % variation in cover estimates between observers in alpine vegetation in 1 m^2 plots.

Several causes of observer error have been identified. The first category is what Morrison (2016) calls "attributes of the observer", e.g. physical and mental fitness/fatigue and experience. But also circumstances like the weather, topography, abundance of mosquitos or even the colour of the soil may play a role (Klimeš et al. 2001; Morrison 2016). A review by Morrison (2016) found mixed results concerning the role of experience, while training of researchers within the study had an overall positive effect on the reliability between observers. Different observers may spend very different amounts of time on one plot, which can have large effects on the completeness of species lists (Morrison 2016). Archaux et al. (2006) found a curvilinear increase of sampling exhaustiveness with sampling time, while the height of the asymptote depended on the observer. The second category are the traits of plants. Rare and small species are more often overlooked (Milberg et al. 2008; Morrison 2016; Futschik et al. 2020; Lisner & Lepš 2020; Morrison et al. 2020; Boch et al. 2022). Those that are easily confounded with similar species are also prone to misidentification (Morrison 2016). The third category are properties of the plot and the vegetation itself. Discrepancies in cover estimation were influenced by the plot size, with inaccuracies increasing above an area of 4 m^2 as it becomes increasingly difficult to get a vertical view of the whole plot (Morrison 2016). However, plot size was not found to have an influence on the errors concerning species identity (Morrison 2016). Lisner & Lepš (2020) found increasing rates of overlooking error with increasing species richness.

There are recommendations to reduce the impact of observer error, although most are rather theoretical because of the high effort involved. Ideally, the same observer would perform all (re)surveys (Morrison 2016). Instead, a frequent recommendation was that several observers should work together to calibrate and train with each other (Klimeš et al. 2001; Morrison 2016; Boch et al. 2022), and even to test and reject those observers that fail to deliver high quality results (Morrison 2016). This should increase the completeness of species lists and average out extreme cover value estimates. To further minimise errors, Klimeš et al. (2001) advised against trying to identify seedlings and very young plants, where error rates have been found to be highest. With a number of precautions, overlooking errors can also be minimised. Taking breaks or limiting the number of surveys per day was recommended to reduce effects of fatigue (Morrison 2016). A very effective method to reduce observer error was to aggregate critical taxa (Boch et al. 2022). A quality control including double sampling of plots and reporting of the resulting pseudo-turnover values was also proposed. This approach promises valuable results but will be out of scope for many studies (Morrison 2016). As an example, with the knowledge about the magnitude of overlooking error, Milberg et al. (2008) were able to compute the minimum difference in occurrences statistically detectable by their surveyors (approx. 9 % when observing 100 plots for *Vaccinium vitis-idea*, for example). Archaux et al. (2006) and Morrison (2016) proposed time control especially on large plots, but the time should be adapted to the richness of the vegetation, e.g. by beforehand identifying species accumulation curves over time from which to estimate the optimum fixed sampling time.

Relocation error

Relocation error is a recurring problem in resurvey studies that can account for a large amount of pseudo-turnover (Kapfer et al. 2017; Verheyen et al. 2018). It results from the difficulty of relocating the exact position of the initially sampled plot. To solve this problem, plots should ideally be physically marked in place when sampled (e.g. by poles or buried magnets), making them “permanent”. While nowadays at least GPS coordinates are usually recorded when sampling a plot, this was not possible in the past. Historical plots therefore often lack exact location information, unless the authors have drawn precise maps and taken notes describing the specific spot. Relocating a plot might still remain difficult in areas of homogeneous vegetation, like grasslands. Kapfer et al. (2017) coined the term “quasi-permanent” for plots with sufficient information on every single plot to allow for an approximate relocation. This also applies to plots with GPS data, which at least limit the location uncertainty to a few meters. Opposed stand non-traceable plots without any information on single plots, where only the general area and the number of plots in the original study may be known.

As far as we are aware, no studies have provided explicit estimates of the magnitude of relocation error. It has often been concluded that relocation errors do not invalidate the overall results of resurvey studies. Kopecký & Macek (2015) reported similar changes in species richness, composition, and frequency of individual species on permanent and quasi-permanent plots in a forest. In dry grasslands, Boch et al. (2019) found an average GPS inaccuracy of 5 m and observed species turnover to increase with GPS inaccuracy. However, their results concerning ecological indicator values were robust to relocation error. In deciduous forests, quasi-permanent plots were relocated by different observers, resulting in an average of 24 m between the relocated plots (Verheyen et al. 2018). In this case, the amount of difference between plots was not dependent on their distance. The results of the resurvey were not affected by the location of the relocated plots. Similarly, Ross et al. (2010) compared the dissimilarities in species composition between several plots at the site of their follow-up survey (spatial dissimilarity) to the amount of species turnover observed in the resurvey (temporal dissimilarity). Here, the temporal pairwise dissimilarity was found to be much greater than the spatial dissimilarity between recent plots. Therefore, they concluded that at least in homogeneous vegetation, accurate trends in vegetation change might still be detectable despite location insecurities. In general, vegetation heterogeneity was identified as an important factor for the relevance of relocation error (Hédl et al. 2017; Kapfer et al. 2017). The size of the plots may additionally play a role, with relocation error presumably being lower in larger plots as fine-scale variabilities average themselves out (Kopecký & Macek 2015).

Although relocation error can be eliminated by using permanently marked plots, in reality these may prove to be less permanent than hoped (Dodd 2011). Aboveground markers can be easily destroyed or moved, (e.g. by animals or floods), over the course of decades. Even below-ground markers like magnets were only retrieved in 87 % of cases in the Countryside Survey of Great Britain (Dodd 2011) and can be confused with other metal in the ground, such as old fence posts. A further recommendation to minimise the uncertainties arising from relocation error is to repeat original relevés several times in slightly different locations. The observed spatial dissimilarities may then be compared with the detected temporal changes (e.g. Ross et al. 2010; Burg et al. 2015). Another related approach is to sample several new plots per initial plot and select the one most similar to the original for further analysis to determine a minimum change estimate (Peppler-Lisbach & Könitz 2017; Harásek et al. 2023). In addition to these methodological recommendations, a technical solution would be to use differential GPS systems with inaccuracies of only a few centimetres in the future (Dodd 2011).

Seasonal Error

Besides the rather well studied relocation and observer error, few studies have focussed on the effect of seasonal variations. These may be particularly important in forests due to the relatively high abundance of vernal geophytes, but also in grasslands (especially in dry grasslands) with high numbers of annual species. Hope-Simpson (1940) found significant differences in the abundance of several species in chalk grasslands, mainly attributed to their flowering period. In woodlands, the frequency of detection differed between seasons for 10 to 20 % of species, with the authors attributing about half of this to chance (Kirby et al. 1986). A systematic study by Vymazalová et al. (2012) found species richness to be highest in summer in forests, with species composition in spring differing significantly from summer and autumn. In dry grasslands, species composition was significantly different in all seasons, while species richness declined in autumn. Only about 50 % of geophytes in forest and a similar proportion of therophytes in dry grasslands could still be recorded in late summer.

1.5.2 Methodological problems with data analysis

Apart from uncertainties arising from the sampling procedure in resurvey studies, analysing the data presents challenges in correctly identifying and interpreting changes in the vegetation. Unlike data obtained under controlled conditions, data collected from field work often include significant levels of noise and stochastic artefacts which have to be accounted for (Palmer 1993; Collins et al. 2000; Zuur et al. 2010). The correct handling of data and analyses in ecology has therefore been the subject of many publications and recommendations on various aspects. For example, Zuur et al. (2010) recommend a thorough data exploration *before* any statistical analyses, to avoid common pitfalls potentially leading to false conclusions (e.g. sorting out outlier measurements when it is probable that these arise from measurement errors or considering collinearity between multiple predictor variables). Especially in the case of resurvey studies, vegetation scientists are dependent on the available historical material. These initial studies were usually not designed for later repetition, but often for phytosociological purposes, which raises a number of potential problems (Diekmann et al. 2007; Lájer 2007). Phytosociological studies often attempt to represent as much of the existing variation in the vegetation as possible, regardless of the respective vegetation type's frequency (Diekmann et al. 2007). Apparently species-rich patches are often preferably selected (Diekmann et al. 2007). Accordingly, in a comparison of randomly vs. non-randomly placed plots, Diekmann et al. (2007) found less rare species in the randomly placed plots, and more very similar plots were sampled with random placement (higher redundancy). Subjectively placed plots represented a larger extent of the existing variation in vegetation composition with the same sampling effort. Lájer (2007) focussed on the implications of non-random sampling for statistical analyses. Most statistical tests (e.g. t-test, Kruskal-Wallis test, Spearman correlation test) are based on the assumption that all observations had the same chance of being included in the dataset and that they were independently sampled (Lájer 2007). In reality, however, the sampled plots are usually not randomly distributed, but were selected according to more or less subjective criteria. Strictly speaking, most statistical tests are therefore not applicable to data sets of classical vegetation samples. However, Lepš & Šmilauer (2007) conclude that with carefully collected data (e.g. with minimised spatial autocorrelation) tests can still validly be used, as is common practise.

Palmer (1993) stressed the importance of non-biased initial sampling for the correct estimation of population size changes and changes in the homogeneity of plots. Populations can be expected to fluctuate in position and size over time, even if there are no long-term trends towards losses or gains. If the initial sampling focussed on patches where rare species were more abundant than on average (which is often the case in traditional vegetation sampling, as shown above), their population sizes or frequencies might be overestimated. In a later follow-up survey, it is likely that the population size will appear to have decreased, simply due to the random fluctuation in time (Palmer 1993). The implications of this “regression to the mean” effect for statistical analyses are part of this thesis in Chapter 4.

The size of available historical data sets, i.e. the number of plots, may also pose limitations to the effectiveness of resurvey studies. The ability to detect significant changes (at a level of $\alpha = 0.05$) depends on the size of the changes, but also on the sample size and the variance in the data (Legg & Nagy 2006). Non-significant results are usually interpreted as “no change”. However, this could be misleading and instead simply reflect that the study design may not have been appropriate to detect a change of the respective magnitude.

1.6 Outline and objectives

Over the past decades, there has been an increase in resurvey studies, particularly due to the growing availability of historical data. However, grassland ecosystems have been underrepresented in these studies. Lasting challenges linked to the resurvey method have been tackled in numerous publications, most notably observer error and location bias. However, methodological struggles remain. Therefore, the main objectives of this thesis were

1. to contribute to the body of knowledge on ecosystem and species changes in grasslands in the light of environmental change (Chapters 2 and 3).
2. to improve the methodology of resurvey studies (Chapters 4 and 5).

Outline

The ecological background to provide context for the issues of biodiversity (loss) in grasslands and the methodology of resurvey studies is given in Chapter 1. A brief summary of the Chapters 2–5, targeting the thesis’ objectives, is presented below. Chapter 6 provides a synthesis of the insights in the previous chapters, and relates them to findings from other studies. The results of the two resurvey case studies are discussed in the light of methodological uncertainties. Implications of the results and future perspectives are given. Appendices to the Chapters 2–5 are presented in Chapter 7.

Chapter 2 gives the results of a classical resurvey study of *Nardus* grasslands and wet heaths in West Germany, 32 years after the initial study. The vegetation was subject to ongoing environmental stressors during the observation period, such as atmospheric deposition and climate change. This study focuses on the role of the exceptionally consistent management on the conservation of the vegetation types under the influence of the mentioned stressors.

Chapter 3 is based on a resurvey study of calcareous grasslands in north-west Germany and focusses on their response to the droughts that have occurred in the observation period. These were exceptionally strong, as is expected to occur more frequently due to ongoing climate change. In particular, the role of topography, i.e. differences between north- and south-facing slopes is analysed.

Chapter 4 tackles a statistical issue in the analysis of resurvey studies and longitudinal experiments. The so-called "regression to the mean" is a phenomenon that occurs regularly when sampling is repeated on the same object. It is widely recognised in the field of medicine, but has so far received little attention in vegetation science. Recommendations on how to deal with this issue when conducting resurvey studies are given.

Chapter 5 is based on a large dataset collected by many collaborators worldwide. It adds to the understanding of noise vs. signal in observed vegetation changes by introducing "baseline turnover" as the amount of stochastic changes in species composition over time. In addition to the theoretical ecological implications, estimates of this background noise may prove useful in interpreting magnitudes of change revealed in resurvey surveys.

Author contributions

The Chapters 2 to 5 were written as independent articles with several co-authors. For all articles, I carried out the statistical analyses, with contributions from Felícia M. Fischer for Mazalla et al. (2024), and wrote the first draft of the manuscripts. Martin Diekmann contributed to the revision of all manuscripts.

The study for Mazalla et al. (2021) and Mazalla et al. (2022b) was designed by Cord Peppler-Lisbach and me. Gerhard Ludwig collected the historical vegetation data and helped with questions regarding the original methodology and plot locations. The fieldwork of the resurvey was carried out by me. Cord Peppler-Lisbach contributed to the interpretation of results as well as revisions of the manuscript.

The scientific question for Mazalla et al. (2022a) was conceived by me and discussed with Martin Diekmann. Cecilia Dupré and Martin Diekmann collected the historical vegetation data and both contributed to manuscript revisions.

For Mazalla & Diekmann (2022), I conceived the statistical question. Martin Diekmann and I contributed to the data collection and discussed the presented concepts.

The scientific question for Mazalla et al. (2024) was developed by me and Martin Diekmann. Felícia M. Fischer, Francesco De Bello, Idoia Biurrun, Rob Brooker, Jörg Brunet, Juan A. Campos, Michele Carbognani, Scott L. Collins, Jiří Danihelka, Pieter De Frenne, Valerio D. Pillar, T'ai G. W. Forte, Frank S. Gilliam, Lars Götzenberger, Daniela Hoss, John T. Hunter, Miklós Kertész, Stefan Klotz, Martin Kopecký, Jan Lepš, Silvia Matesanz, Timothy Ohlert, Gábor Ónodi, Robin J. Pakeman, Cord Peppler-Lisbach, Alessandro Petraglia, Wolfgang Schmidt, Ute Schmiedel, Marta Gaia Sperandii, Enrique Valencia, Karsten Wesche, and Martin Zobel contributed to the data collection. All authors contributed to the revisions of the manuscript.

1.7 List of publications

Mazalla, L., Ludwig, G. & Peppler-Lisbach, C. (2021) ‘Nardus grasslands and wet heaths are affected differently by reintroduction of management and pH recovery’. *Tuexenia* 41, 227–252. DOI: `10.14471/2021.41.010`.

Mazalla, L. & Diekmann, M. (2022) ‘Regression to the mean in vegetation science’. *Journal of Vegetation Science* 33.2, e13117. DOI: `10.1111/jvs.13117`.

Mazalla, L., Diekmann, M. & Dupré, C. (2022a) ‘Microclimate shapes vegetation response to drought in calcareous grasslands’. *Applied Vegetation Science* 25.3, e12672. DOI: `10.1111/avsc.12672`.

Mazalla, L., Ludwig, G. & Peppler-Lisbach, C. (2022b) ‘Vegetationsveränderungen in Borstgrasrasen im Kreis Euskirchen (Nordeifel) – Eine Wiederholungsstudie nach 32 Jahren’. German. *Treffpunkt Biologische Vielfalt.* Jubiläumsband. 20 Jahre interdisziplinärer Forschungsaustausch im Rahmen des Übereinkommens über die biologische Vielfalt. Ed. by R. Schliep & J. Stadler. Vol. 632. BfN-Schriften, pp. 29–31. DOI: `10.19217/skr632`.

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Peppler-Lisbach, C., Kratochwil, A., Mazalla, L., Rosenthal, G., Schwabe, A., Schwane, J. & Stanik, N. (submitted) ‘Synopsis of Nardus grassland resurveys across Germany: eutrophication and rising soil pH as consistent patterns?’ *Journal of Vegetation Science.*

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— Chapter 2 —

Nardus **grasslands and wet heaths are affected differently by reintroduction of management and pH recovery**

Leonie Mazalla, Gerhard Ludwig & Cord Peppler-Lisbach (2021)
Tuexenia, 41: 227–252
https://doi.org/10.14471/2021.41.010

Nardus grassland with *Pedicularis sylvatica, Genista anglica, Lathyrus linifolius, and Luzula congesta*

Abstract

Semi-natural habitats in temperate regions are local hotspots of biodiversity, but multiple stressors such as land use change and atmospheric deposition pose a threat to the existence and functioning of these ecosystems. We conducted a resurvey of *Nardus* grasslands and wet heaths in the Eifel mountains to monitor the development of these habitats under the influence of a long-term management regime and the above-mentioned stressors. Surveys of 50 plots of *Nardus* grasslands and 14 of wet heaths from 1986 were repeated in 2018. Prior to the first survey, the meadows had lain fallow for approx. 30 years. Shortly afterwards, they were re-entered into a management program with annual mowing from mid-July. We found significantly increased soil pH values from an average of 3.9 up to 4.6 since the 1980s, following the reduction in SO_2-depositions. Ellenberg indicator values for soil reaction and nutrients increased significantly in the wet heaths but stayed relatively stable in the *Nardus* grasslands. All meadows that were *Nardus* grasslands in 1986 could still be identified as such, with high total species numbers and a high proportion of character species. However, cover sums of these declined, while more species typical of agricultural grasslands and small sedge fens occurred. Low-competitive species (e.g. *Carex pilulifera*, *Pedicularis sylvatica*) profited, while species that can gain dominance in fallow situations (esp. *Molinia caerulea*) were pushed back. The consistent management of the sites contributed essentially to this outcome by effectively counteracting eutrophication. The relatively early date of mowing enabled a successful removal of nutrients and resulted in a characteristic structure and species composition. However, some quantitative changes indicate a risk of eutrophication and that continuing management will be crucial for a sustained conservation of *Nardus* grasslands. The same management, however, was not equally able to preserve wet heaths, which had been largely transformed into wet varieties of *Nardus* grasslands, small sedge-dominated swards or wet meadows with signs of eutrophication. Other management strategies (e.g. periodic top soil removal, possibly combined with extensive grazing) should be considered. In any case, we recommend further monitoring to secure the survival of these important remnants of historical land use.

Keywords Eifel, eutrophication, long-term vegetation change, nitrogen deposition, resurvey, sulphur deposition

2.1 Introduction

Semi-natural habitats are local hotspots of biodiversity in temperate regions whose landscapes are severely affected by species loss (Habel et al. 2013; Dengler et al. 2014). They offer rare refuges for specialised species of nutrient-poor sites. Multiple stressors pose a threat to the existence and functioning of these habitats. Changed land use practices have considerably reduced the extent of semi-natural and nutrient-poor ecosystems over the last century (Leuschner & Ellenberg 2017b). The usage of suitable areas has been intensified by fertilising and drainage, while most less productive sites were abandoned or afforested (Poschlod et al. 2005). Global warming and atmospheric depositions, recently especially of nitrogen and in the past also of sulphur oxide, have been additional drivers of vegetation change (Sala et al. 2000).

The habitats considered in this study are species-rich *Nardus* grasslands (*Nardetalia strictae* Preising 1950) and wet heaths (*Ericion tetralicis* Schwickerath 1933 and *Oxycocco-Ericion* Nordhagen 1936). They are protected under European law as FFH habitat types (No. 6230, prioritary, “Species-rich *Nardus* grasslands” and No. 4010, “Northern Atlantic wet heaths with *Erica tetralix”*). Their conservation status in Germany is stated as “unfavourable – bad” with a worsening trend (BfN 2019). Out of 105 species listed by Ellenberg et al. (1992) as character species of *Nardus* grasslands and wet heaths, 64 % are currently included as threatened in the Red List of Germany (Metzing et al. 2018).

To our knowledge there are few long-term studies on current vegetation changes of *Nardus* grasslands, and even fewer for wet heaths. The available studies originate from different regions in Europe, but with a strong focus on the UK, and cover different time spans between the middle of the 20th century and the early 2000s. Some general trends were described in the majority of long-term resurvey studies: The diversity of the habitats was commonly described as degrading, with a decrease in the number of characteristic species and an increase in Ellenberg indicator values for nutrients (Dupré et al. 2010; McGovern et al. 2011; Britton et al. 2017; Peppler-Lisbach et al. 2020). In some cases, graminoid species have increased at the expense of forbs (Dupré et al. 2010; McGovern et al. 2011); in other cases, generalist and more competitive species have increased (Britton et al. 2017; Peppler-Lisbach et al. 2020). The main drivers of community changes were reported to be nitrogen and sulphur depositions, as well as the reduction of management intensity.

Deposited nitrogen levels currently exceed the threshold for critical loads from atmospheric deposition (10–20 kg N ha^{-1} a^{-1} for *Nardus* grasslands and wet heaths), in most parts of Europe (Bobbink et al. 2011). Typical effects of reactive nitrogen deposition are known to be a general loss of biodiversity, an increased graminoid:forb ratio (Field et al. 2014; Stevens et al. 2006), a decrease in evenness, and an increase in more nutrient-demanding species of agricultural grasslands (De Graaf et al. 2009; Bobbink et al. 2010; Stevens et al. 2010; Stevens et al. 2011; Southon et al. 2013). As nitrogen-induced eutrophication facilitates higher productivity, species that are able to react to increased nutrient availability with high growth rates outcompete those adapted to nutrient-poor environments (Bobbink et al. 1998; Roem & Berendse 2000; De Graaf et al. 2009). Another effect of nitrogen deposition is acidification, especially due to ammonium (NH_4^+). As a consequence, rare species, which are often typical of intermediate pH values, decline, in favour of acid-resistant species that are more often grasses (Bobbink et al. 1998; Kleijn et al. 2008; Maskell et al. 2010).

In contrast to nitrogen deposition, which persists on a high level, sulphur oxide emissions have been significantly reduced in the last decades due to effective air pollution policies (UBA 2019). As a consequence, pH levels have recently been found to be recovering (Kirk et al. 2010; McGovern et al. 2011; Mitchell et al. 2018; Peppler-Lisbach et al. 2020). McGovern et al. (2011) found that the vegetation response to recovery from acidification is lagging behind by decades, as soil parameters such as exchangeable cations still reflect an earlier, more acid, state. The more recent studies by Britton et al. (2017) and Peppler-Lisbach et al. (2020) however, found a significant increase of acid-sensitive species.

Here, we present the results of a resurvey of both the vegetation and the soil chemistry of plots first surveyed in 1986 in *Nardus* grasslands and wet heaths in the Eifel mountains in West-Germany. All of the study sites were mown for the last 30 years, with one cut from mid-July. The local conditions of the sites are very well controlled, with a strict conservation status, no drainage or fertilising, and a management regime in place that aims to maintain the typical vegetation structure and diversity. However, global and regional influences cannot be controlled. This study offers an opportunity to explore the long-term effects of well-planned and -conducted conservation practices in valuable habitats under the stress of global and regional drivers.

We expect a shift in species composition indicating eutrophication and less acidic conditions due to (1) recovery of pH values as a result of sulphur emissions that were high in the past but have been reduced for decades, and (2) eutrophication caused by ongoing high N-depositions. We further expect that (3) the implemented management regime of regular mowing has generally preserved the typical structure and species composition of vegetation.

2.2 Materials & Methods

2.2.1 Study area

The study area is located in the west of Germany in the Eifel Mountains, approx. 50 km south-west of the city of Bonn. It presents the northernmost part of the Rhenish Slate Mountains with predominantly siliceous bedrock (sandstone, clay shales, greywacke). These substrates weather to nutrient-poor soils with low pH values containing a water-retaining soil horizon due to their high clay content (Meynen & Schmitthüsen 1953 - 1962). The altitude of the study plots varies from 500 to 605 m a.s.l. The climate is of a sub-oceanic character, with a mean annual precipitation of 800–900 mm and a mean annual air temperature of 7.7 °C (DWD CDC 2018). Individual relevés were from nine different meadow sites dispersed over an extent of approx. 18 km × 5 km and isolated from each other in the landscape. The size of the single sites ranges from 0.4 to 4.8 ha. All study sites are protected under federal law as nature reserves, and most of them additionally under European law as Natura 2000 sites (Kreis Euskirchen 2003; Kreis Euskirchen 2005). Except for one site, there is no intensive agricultural use taking place in the direct vicinity, i.e. there is no or no strong input of fertilizer from agricultural sites and a low chance of species of intensively used grasslands to invade the swards. In most cases, the sites were surrounded by coniferous forest. At the time of the initial survey in 1986, the meadows had been abandoned for approx. 30 years (Ludwig 1987). Soon afterwards, all sites were entered into a management program with contractual nature conservation, and have since been mown once a year from mid-July (Schumacher et al. 2007; BioStation 2019b). Additionally, two EU-funded projects for the maintenance of heaths and *Nardus* grasslands were conducted in the area (BioStation 2018; BioStation 2019a). They comprised measures such as clearing shrubs and blocking off ditches to restore a more natural water regime. The reactive nitrogen deposition level, currently 11–12 kg N ha^{-1} a^{-1} (UBA 2021), lies in the range of critical loads that have been described for acid grassland and wet heath.

2.2.2 Data sampling

The resurvey is based on relevés made in 1986 by Gerhard Ludwig (Ludwig 1987). This data basis was very well suited for a revisitation study. The methods of the original study were well documented and the author could be won as co-author for the resurvey study. In 2018, 50 relevés of *Nardus* grasslands (*Violion caninae* Schwickerath 1944: *Violenion caninae* Peppler-Lisbach & Petersen 2001, *Juncenion squarrosi* Peppler-Lisbach & Petersen 2001 and *Galium-saxatile-Nardus-stricta* community, Peppler-Lisbach & Petersen 2001) and 14 plots of groundwater-influenced wet heaths (*Ericion tetralicis* Schwickerath 1933 and *Oxycocco-Ericion* Nordhagen ex Tx.1937) were resampled. Precisely drawn maps with a thorough documentation of plot locations were used (scale 1:5000, pseudo-permanent following Kapfer et al. 2017). These were geo-referenced with ArcGIS (ESRI 2012). The resulting coordinates were located in the field using a differential GPS with an accuracy of up to 2 cm. While resampling, we avoided small-scale heterogeneity created by vehicle lanes or small depressions, to obtain homogeneous plots (as this has been done in the initial study in the same way). In the case of five plots overgrown by shrubs, the original location was shifted by a few meters. The plots sampled in 2018 were permanently marked by magnets in two diagonal corners. The plot size was 20 m^2. Species cover values were estimated using a modified Braun-Blanquet scale in which the lower classes “r”, “+”, and “1” were classified based only on percent cover and not on number of individuals (Ludwig 1987).

Mixed soil samples from 1–10 cm depth were taken from every plot and soil pH was measured in deionised water. Additional data on ortho-phosphate were available for 22 plots. In 1986, these had been measured directly in soil water extracted by suction cups. Direct extraction of soil water was not possible in 2018 due to dry weather conditions; we therefore created an equilibrium soil solution from soil samples as a substitute (Richards 1954; Blume et al. 2011). Ortho-phosphate was measured with a photometer, with a measuring range of 15–1000 µg P l^{-1} after filtering the soil solution with a mesh width of 0.45 µm. Conductivity (in µS cm^{-1}) was measured in the equilibrium soil solution with a probe.

2.2.3 Data analysis

All data was organised with Turboveg (Hennekens & Schaminée 2001), the analyses were conducted with R and Rstudio (RStudio Team 2016; R Core Team 2020), including the packages vegdata (Jansen & Dengler 2010), vegan (Oksanen et al. 2019), hier.part (Nally & Walsh 2004), exactRankTests (Hothorn & Hornik 2019), car (Fox & Weisberg 2019), nortest (Gross & Ligges 2015), ggplot2 (Wickham 2016) and reshape2 (Wickham 2007). All species names were harmonised according to the GermanSL1.3 (Jansen & Dengler 2008; Jansen & Dengler 2010). A few taxa that were identified to different levels in the two surveys were merged to aggregates: *Festuca rubra* agg., *Centaurea jacea* agg. and *Dactylorhiza maculata* agg.

To account for initial floristic differences between plots in 1986, which might have influenced subsequent changes, we classified the plots into *Nardus* grassland (syntaxon N) and wet heath (syntaxon WH). For all relevés, mean presence-absence based and community weighted (after square root transformation of cover) Ellenberg indicator values for temperature (mT), soil moisture (mF), soil reaction (mR), and soil nitrogen (mN) were calculated (Ellenberg et al. 1992).

We classified species into seven groups according to their habitat preference (Table A8 in Supplement), following Ellenberg et al. (1992) and for moss species Dierssen (1982) unless indicated otherwise: 1. NardG, character species of *Nardus* grasslands (class *Calluno-Ulicetea* Br.-Bl. et Tüxen 1943 ex Klika et Hadac 1944, according to Peppler-Lisbach & Petersen (2001)); 2. WetH, character species of wet heaths (*Oxycocco-Sphagnetea* Br.-Bl. & Tx. ex Westhoff et al. 1946); 3. SSF, character species of small sedge fens (*Scheuchzerio-Caricetea nigrae* Tx. 1937); 4. AgriG, species of agricultural grasslands (*Molinio-Arrhenatheretea* Tx. 1937, with N.EIV values > 3); 5. PoorG, other species of nutrient-poor grasslands with N.EIV values $<= 3$ not included in NardG; 6. Aban, abandonment indicators like trees, bushes, and typical understorey species; 7. I, indifferent species. All species were additionally classified into groups according to taxonomy and growth form: 1. dicotyl herbs, 2. graminoids, 3. trees/bushes, 4. dwarf shrubs, 5. monokotyle herbs, 6. mosses.

Variable changes were calculated as $\Delta variable = var2018 - var1986$. Tests on the significance of parameter changes (e.g., ΔpH, Δcover sums of character species) were conducted using a Wilcoxon signed rank test. Changes of individual species (abundance and cover) were also tested for significance, with p-values corrected for the number of species considered (controlling the false discovery rate, fdr, Benjamini & Hochberg 1995). Only species that occurred at least ten times in the dataset were included.

Species "gain" and "loss", as indices for species turnover, were calculated with
$gain = newspec / specnum2018$
and
$loss = lostspec / specnum1986$
where *newspec* is the number of species in a 2018 relevé that were not present in the corresponding plot in 1986 and *lostspec* is the number of species in a 1986 relevé that were no longer found in the corresponding plot in 2018. *Specnum* is the total number of species in the respective years. Evenness was calculated as a measure for the dominance structure of species in the relevés (Pielou 1966). Sørensen dissimilarities based on presence/absence data, as well as cover values, were also computed (Borcard et al. 2018). A fallow index for each plot was calculated as a sum of square-root transformed cover values of all fallow indicator species (species group Aban) and *Molinia caerulea* as a species gaining dominance in abandoned meadows.

A DCA of all relevés from 1986 and 2018 was performed with the function "decorana" (package vegan) from presence/absence data, without down-weighting of rare species. We calculated the best multiple linear regression models for changes in species richness (total, vascular, and bryophytes), Sørensen dissimilarity (quantitative and qualitative), ΔmR and ΔmN, as well as changes in frequency and cover sums of the species groups NardG, SSF, AgriG and PoorG as dependent variables. Explaining variables included in the full model were: pH1986, ΔpH, fallow-index1986, and site. Models for ΔmR and ΔmN also included mF1986 and ΔmF as a surrogate for soil moisture. F- and R- or N-values of the present species were not correlated, i.e. species of wetter sites did not have higher or lower R- or N-values. Interaction terms with syntaxon (wet heath/*Nardus* grassland) were included for all variables except site. Nitrogen or sulphur-oxide deposition were not included as predictor variables, because they are largely uniform across the study region and therefore cannot explain local differences. The same applies to the management regime. Variables were selected by stepwise elimination with the "step"-function based on Bayes Information Criterion (BIC). Dependent variables of models whose residuals did not follow a normal distribution were rank-transformed (ΔSSF.pa, Δspecnum.bryo). Models for ΔmR and ΔmN showed an outlier outside the "Cook's distance" metric of 0.5, which has an extreme ΔpH of 2.4 that might be a measurement error, and in one case the influence of one single species with very high N-value (*Epilobium angustifolium*, N = 8). This outlier data point was removed for the final model.

To examine variable effects on overall vegetation change, we conducted a Permanova based on Euclidean distances of a matrix of species differences between the years. For this, we used the rda function of the package vegan, including permutation testing, as it offers automatic variable selection. To obtain the species-differences matrix, square-root transformed cover values of species per plot in 1986 were subtracted from the respective values in 2018. The same procedure was used for presence/absence data.

2.3 Results

2.3.1 Soil variables and mean indicator values

Across all sites, between 1986 and 2018, mean pH value showed a significant increase from 3.87 to 4.62 (Figure 2.1). The range in which aluminium toxicity plays a role (pH < 4.5, Scheffer & Schachtschabel 2010) was reached for 98 % of the plots in 1986, while this was only the case for 22 % in 2018. The change in pH values was negatively dependent on initial pH values (estimate: -0.72, R^2: 0.33, $p < 0.001$), i.e. the more acid the soils were in 1986, the more the pH values increased until 2018. Additionally, increasing soil moisture, estimated as difference in mean mF, had a positive effect on the change in pH values (estimate: 0.23, R^2: 0.13, $p = 0.002$). Wet heaths had lower pH values than *Nardus* grasslands in both survey years but the increase in pH did not differ between the syntaxa. mN and mR values showed significant differences between both community types in 1986, but not in 2018 (Table A1 in Supplement). Mean ortho-phosphate levels in soil water decreased significantly over time. Over all sites, they were on average 15 µg P l^{-1} in 1986. In 2018, 10 out of the 22 samples were under the detection limit of 15 µg P l^{-1}, the remaining 12 samples having an average of 27 µg P l^{-1}.

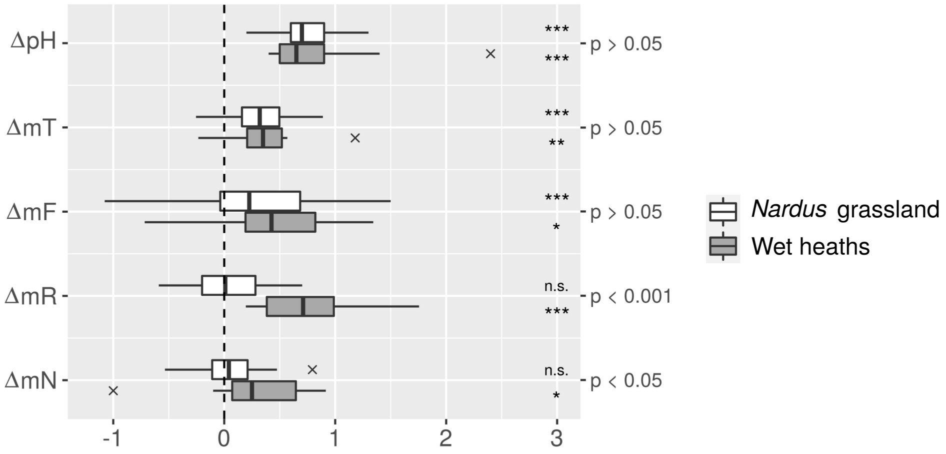

Figure 2.1: Changes (Δ) of pH and presence/absence-based Ellenberg indicator values for temperature (mT), soil moisture (mF), soil reaction (mR) and soil nutrients (mN). Significance symbols (*** p<0.001 ** p<0.01 * p<0.05 n.s. p>0.05) indicate differences in indicator values between 1986 and 2018. Out-written p-values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.

Abbildung 2.1: Veränderung (*Delta*) von pH-Wert und ungewichteten Ellenberg-Zeigerwerten für Temperatur (mT), Bodenfeuchte (mF), Bodenreaktion (mR) und Nährstoffe (mN). Sternchen (*** p<0,001 ** p<0,01 * p<0,05 n.s. p>0,05) geben das Signifikanz-Niveau von Unterschieden der Zeigerwerte zwischen 1986 und 2018 an. Ausgeschriebene p-Werte geben die Signifikanz von Unterschieden in der Veränderung zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.

Mean unweighted indicator values for soil reaction and nutrients showed significant increases in the wet heath plots, while those of *Nardus* grassland remained comparatively stable over the study period (Figure 2.1). The increases in mR and mN in *Nardus* grasslands were only significant for cover-weighted indicators (Figure A1 in Supplement). Although the increase in pH values did not differ significantly between the syntaxa, the increase in mR and mN was significantly higher in the wet heath plots (Figure 2.1). Mean unweighted indicator values for temperature and moisture showed significant increases across all plots, from a mean $mF_{1986} = 5.8$ to a mean $mF_{2018} = 6.1$, and a mean $mT_{1986} = 4.2$ to a mean $mT_{2018} = 4.5$.

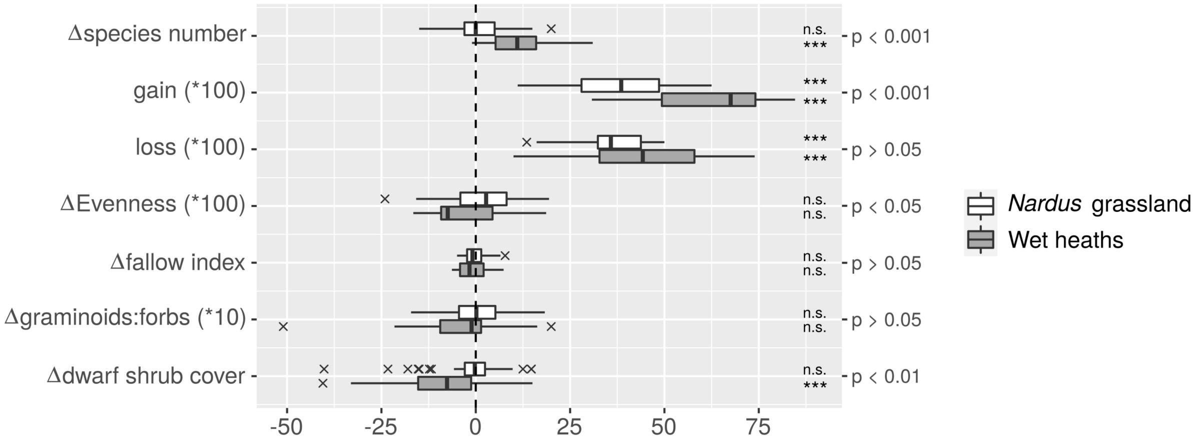

Figure 2.2: Changes (Δ) in parameters describing biodiversity and structure between 1986 and 2018. Significance symbols (*** p<0.001 ** p<0.01 * p<0.05 n.s. p>0.05) indicate differences in variables between 1986 and 2018. Out-written p-values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.

Abbildung 2.2: Veränderungen (Δ) in Parametern betreffend Biodiversität und Struktur zwischen 1986 und 2018. Sternchen (*** p<0,001 ** p<0,01 * p<0,05 n.s. p>0,05) geben das Signifikanz-Niveau von Unterschieden der Variablen zwischen 1986 und 2018 an. Ausgeschriebene p-Werte geben die Signifikanz von Unterschieden zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.

2.3.2 Biodiversity and vegetation structure

All *Nardus* grasslands from 1986 were still typical *Nardus* grasslands in 2018, with high total species numbers (mean 34.3 / 20 m^2), and a high proportion of character species (on average 40 % of total species, with 31 % share of total cover). Total species numbers did not change significantly (Figure 2.2). Broken down into vascular plants and bryophytes, vascular plant richness increased by on average 4.1 species per plot, while bryophytes declined by on average 3.3 species per plot. However, there was a gradual shift to more nutrient-demanding, mesophilous species. Floristic changes were much greater in the plots that originally contained wet heaths. In 1986, 15 % of all species were character species of wet heaths, with a share of cover of 34 % per plot. In 2018, these shares amounted to only 3 % typical species, with a mean share of cover of 4 %. Here, total species numbers rose from $\text{mean}_{1986} = 24.6$ to $\text{mean}_{2018} = 36.6$ species per plot, with vascular plant numbers increasing on average by 12.8 species and bryophytes decreasing by 0.7 species per plot. Species turnover was significantly higher in the wet heaths, with a mean gain of 0.62 and a mean loss of 0.45, meaning that 62 % of the species in the relevés of 2018 were not present in 1986, and 45 % of species in the relevés of 1986 were lost in 2018. For the *Nardus* grasslands, these numbers amounted to a gain of 0.38 and a loss of 0.37.

Between 1986 and 2018, evenness increased slightly in *Nardus* grasslands but not in wet heaths, while the fallow index decreased slightly (Figure 2.2). The graminoids:forbs ratio showed no significant change across all plots. The number and cover of dwarf shrubs in wet heaths was significantly reduced from on average 2.8 species with a cover sum of 21 % in 1986, to 1.6 species with a cover sum of 13 % in 2018.

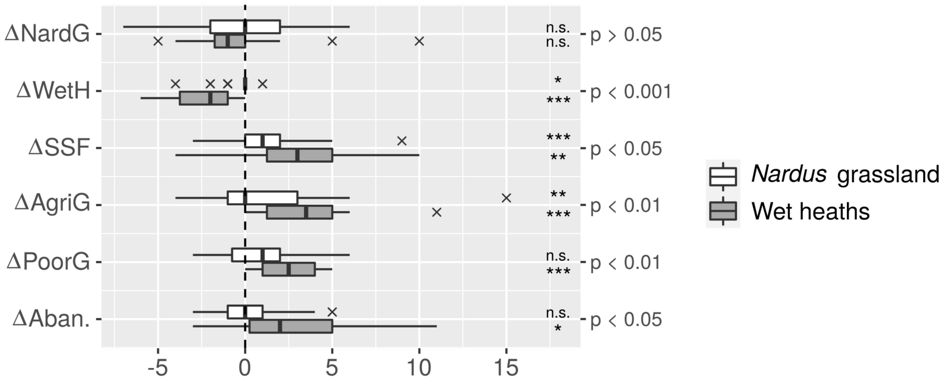

Figure 2.3: Changes (Δ) in species numbers of several species groups: NardG = character species of *Nardus* grasslands; WetH = character species of wet heaths; SSF = character species of small sedge fens; AgriG = species of agricultural grasslands; PoorG = other species of nutrient-poor grasslands; Aban = fallow indicators. Significance symbols (*** p<0.001 ** p<0.01 * p<0.05 n.s. p>0.05) indicate differences in species numbers between 1986 and 2018. Out-written p-values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.

Abbildung 2.3: Veränderung in der Frequenz von Arten der jeweiligen Artengruppen: NardG = Charakterarten der Borstgrasrasen; WetH = Charakterarten der Feuchtheiden; SSF = Charakterarten der Kleinseggenriede; AgriG = Arten des Wirtschaftsgrünlands; PoorG = andere Arten mageren Grünlands; Aban = Brachezeiger. Sternchen (*** p<0,001 ** p<0,01 * p<0,05 n.s. p>0,05) geben das Signifikanz-Niveau von Unterschieden der Artenzahlen zwischen 1986 und 2018 an. Ausgeschriebene p-Werte geben die Signifikanz von Unterschieden zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.

2.3.3 Species groups according to habitat preference

The number of *Nardetalia* character species (NardG) was unchanged in *Nardus* grasslands (Figure 2.3), though their cover sums decreased significantly (Figure A2 in Supplement). More species of agricultural grasslands (AgriG), nutrient-poor grasslands (PoorG) and small sedge fens (SSF) appeared in the relevés in 2018 compared to 1986, but cover sums only increased significantly for the SSF-group. The species composition of wet heaths in the study area changed more drastically. The number and cover sums of wet heath character species (WetH) decreased in every relevé. The groups SSF, AgriG, PoorG and Aban increased significantly in numbers and the groups SSF, as well as AgriG also in cover.

2.3.4 Individual species

Comparisons of the prevalence of individual species showed that in *Nardus* grasslands, ten species had significantly increased in either frequency or cover, or both (Table A2 in Supplement). Two small sedge species (*Carex pilulifera* and *Carex echinata*) and the two hemiparasites *Pedicularis sylvatica* and *Rhinanthus minor* showed the strongest increases. *Rhytidiadelphus squarrosus* increased most in cover. Not reflected in the list of significantly increasing species are a number of agricultural grassland species (n = 11) that have only recently appeared in the sites, but are still very rare (e.g. *Cerastium holosteoides*, *Trifolium pratense*, *Vicia cracca*). Eleven species significantly decreased, more than half of which were mosses. Of the decreasing species, 55 % belong to the *Nardetalia* character species group (NardG). The frequency of *Arnica montana* decreased from 74 % to 52 % of all plots, while its mean cover values declined by 80 %. *Nardus stricta* showed the strongest decline in cover, but no change in frequency. The cover of *Molinia caerulea* decreased by on average 35 %, however, this was not significant.

In the 14 wet heath sites, only two species (*Rhytidiadelphus squarrosus* and *Agrostis canina*) showed significant increases, while *Erica tetralix* decreased significantly in cover (Table A3 in Supplement). Mean indicator values for temperature, soil moisture, soil reaction, and nutrients did not differ significantly between increasing and decreasing species of both initial syntaxa. The number of vascular plant species included in the Red List of Germany (Metzing et al. 2018) increased from 29 to 32 over all plots, with more than half of the endangered species in 2018 being characteristic species of *Nardus* grasslands and wet heaths.

2.3.5 Multivariate Analysis

The DCA containing all monitored plots from 1986 and 2018 supports the result that in the study period, wet heaths have changed more drastically than *Nardus* grasslands (Figure 2.4). While the contours outlining all *Nardus* grassland plots in 1986 and 2018 show a considerable overlap, the contours surrounding the wet heath plots in 1986 and 2018 only overlap slightly. The first axis of the DCA represents a nutrient/pH-gradient, with typical species of agricultural grasslands increasingly occurring in the negative part of the axis, together with higher mR- and mN-values, pH, and total species numbers. The second axis describes a soil moisture gradient, being closely positively correlated with mF indicator values and character species of small sedge fens, and negatively correlated with typical species of *Nar-*

dus grasslands. Both contours have shifted towards more moist and nutrient-rich conditions. In addition, floristically, plots of wet heath and *Nardus* grassland have become more similar: In 1986, contours outlining the separate syntaxa did not overlap, while they share about a third of their area in 2018.

Table 2.1: Coefficients (arrow pointing up: positive, arrow pointing down: negative) of multiple linear models for differences in presence/absence-based (p/a) and cover weighted Ellenberg indicator values for soil acidity (mR) and nutrients (mN) between 1986 and 2018. pH 1986, Fallow index 1986, mF 1986: pH, fallow index, and mF as measured in 1986. ΔpH, ΔmF: Changes of pH and mF between 1986 and 2018. Wet heath: syntaxon as compared to reference category *Nardus* grasslands. Site: all 8 sites as compared to reference category site 1.

Tabelle 2.1: Koeffizienten (Pfeil nach oben: positiv, Pfeil nach unten: negativ) der multiplen linearen Modelle für Differenzen von Präsenz/Absenz-basierten (p/a) und Deckungsgrad-gewichteten (cover) Ellenberg-Zeigerwerten für Bodenreaktion (mR) und Nährstoffe (mN) zwischen 1986 und 2018. pH 1986, Fallow index 1986, mF 1986: pH, Bracheindex und mF von 1986. ΔpH, ΔmF: Differenz der pH-Werte und mF zwischen 1986 und 2018. Wet heath: Syntaxon Feuchtheide im Verhältnis zur Bezugskategorie Borstgrasrasen. Site: Alle 8 Gebiete im Verhältnis zur Bezugskategorie Gebiet 1.

	R^2	pH 1986	ΔpH	Fallow index 1986	mF 1986	ΔmF	WH:mF 1986	WH: ΔmF	WH:pH 1986	Wet heath	Site
ΔmR p/a	0.38***									⇑***	
ΔmR cover	0.24***	⇑			⇑*				⇑**	⇓**	
ΔmN p/a	0.44***				⇓	⇓	⇑*	⇓*		⇓	⇓⇑***
ΔmN cover	0.08***		⇑*								

2.3.6 Influence of site conditions on vegetation change

The results of the linear regression models showed which environmental variables had a significant effect on the changes in vegetation composition. Site and syntaxon were also included in the models, to account for local conditions and for initial differences between *Nardus* grasslands and wet heaths (see Supplement Tables A1 – A3 for detailed model coefficients). For most dependent variables, the largest part of explained variance was accounted for by the differences between syntaxa or between sites. Increases of pH positively influenced cover-weighted changes in mN (Table 2.1), and were related to a higher presence/absence-based Sørensen-dissimilarity, increasing numbers of total vascular species, agricultural grasslands species, and small sedge sward species, but not their respective cover sums (Table 2.2). The rise in pH had a negative effect on the cover sums of *Nardetalia* character species which were, additionally, positively influenced by the fallow-index in 1986. A higher fallow index in 1986 also led to a higher qualitative Sørensen-dissimilarity, while numbers of bryophytes were reduced more strongly.

Variable selection in RDA revealed changes in pH, mF, and site as important variables influencing presence/absence-based vegetation change, with a total of 29 % explained variance (Table A7). Individually, changes in pH explained only 3 % of the total variance in the dataset of species differences, while 22 % could be attributed to differences between the nine sampling sites. For differences in species cover values, changes in pH had no significant effect in the RDA. Changes in mF, the fallow-index$_{1986}$, syntaxon, and site together explained 42 % of total variance, with the majority (22 %) again accounted for by differences between sites. The syntaxon explained 5 % of the total variance. No interaction terms between syntaxon and other variables were significant.

Table 2.2: Coefficients (arrow pointing up: positive, arrow pointing down: negative) of multiple linear models for differences in species numbers of all species (total), vascular species, and bryophytes, quantitative and qualitative Sørensen dissimilarity, and differences of species group, species numbers (p/a), and cover sums (cover) between 1986 and 2018. NardG = Nardetalia character species, AgriG = agricultural grassland species, SSF = species of small sedge fens, PoorG = other species of nutrient-poor grasslands. pH 1986, Fallow index 1986: pH and fallow index as measured in 1986. ΔpH = Change of pH between 1986 and 2018. Wet heath = syntaxon as compared to reference category *Nardus* grasslands. Site = all 8 sites as compared to reference category site 1. Models without significant results are not listed in the table: Sørensen quantitative, ΔNardG p/a, ΔAgriG cover, ΔSSF cover, ΔPoorG cover.

Tabelle 2.2: Koeffizienten (Pfeil nach oben: positiv, Pfeil nach unten: negativ) der multiplen linearen Modelle für Differenzen von Artenzahlen (species numbers) aller Arten (total), der Gefäßpflanzen (vascular) und der Moosarten (bryophytes), der quantitativen und qualitativen Sørensen-Unähnlichkeit, sowie der Differenzen von Artenzahlen (p/a) und Deckungssummen (cover) der soziologischen Kennartengruppen. NardG = Charakterarten der Borstgrasrasen, AgriG =Arten des Wirtschaftsgrünlands, SSF = Charakterarten der Kleinseggenriede; PoorG = andere Arten mageren Grünlands. pH 1986, Fallow index 1986 = pH und Bracheindex von 1986. ΔpH = Differenz der pH-Werte zwischen 1986 und 2018. Wet heath = Syntaxon Feuchtheide im Verhältnis zur Bezugskategorie Borstgrasrasen. Site = Alle 8 Gebiete im Verhältnis zur Bezugskategorie Gebiet 1. Modelle ohne signifikante Ergebnisse sind nicht in der Tabelle aufgeführt: Sørensen quantitative, ΔNardG p/a, ΔAgriG cover, ΔSSF cover, ΔPoorG cover.

	R^2	pH 1986	ΔpH	Fallow index 1986	WH: pH 1986	Wet heath	Site
Species numbers							
Δspecies numbers total	0.28***					⇑***	
Δspecies numbers vascular	0.27***		⇑*			⇑***	
Δspecies numbers bryophytes	0.19***			⇓*		⇑***	
Sørensen qualitative	0.41***	⇑*	⇑*	⇑**		⇑***	
Species groups							
ΔNardG cover	0.47***		⇓*	⇑**		⇓*	⇑⇓***
ΔAgriG p/a	0.13**		⇑*			⇑*	
ΔSSF p/a	0.15**		⇑*			⇑*	
ΔPoorG p/a	0.19**	⇓*			⇑*	⇓*	

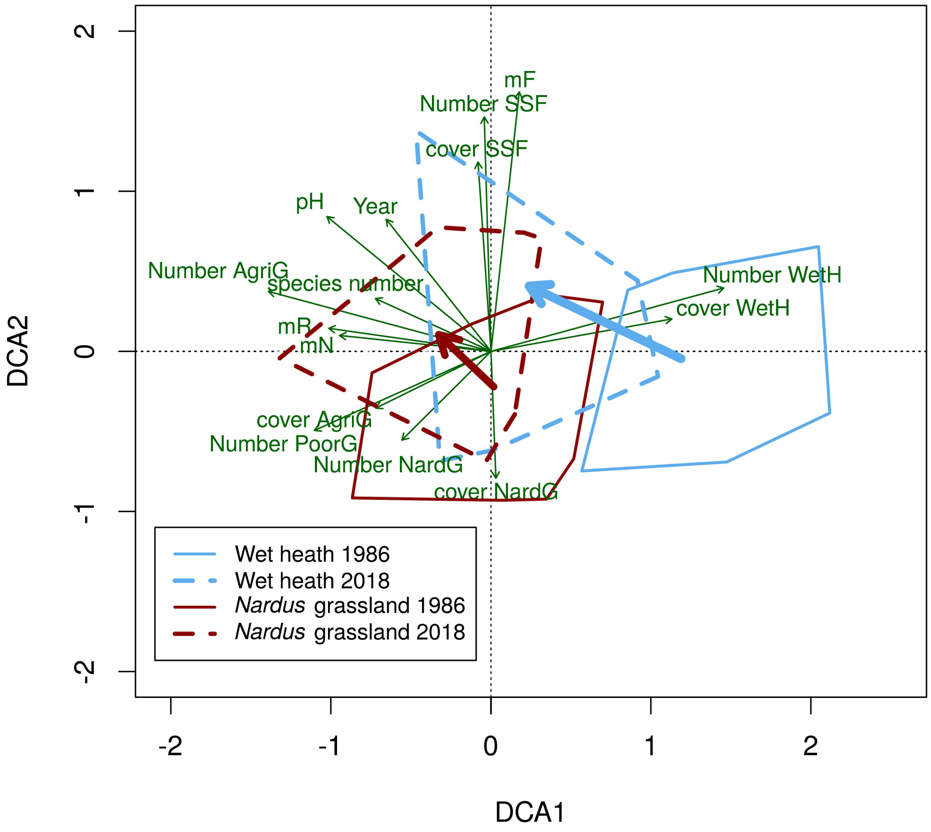

Figure 2.4: DCA of all plots in 1986 and 2018, based on species presence/absence data. Red contours outline *Nardus* grasslands and blue contours wet heaths, with continuous outlines being the 1986 plots and dotted outlines the 2018 plots. Environmental variables included are significantly correlated to one of the DCA axes ($p < 0.05$) and with $R^2 \geq 0.15$. mF, mR, mN: Presence/absence-based Ellenberg indicator values for soil moisture, soil reaction, and nutrients; Species numbers (Number) and cover sums (cover) of following species groups: NardG = Nardetalia character species, WetH = wet heath character species, SSF = species of small sedge fens, AgriG = agricultural grassland species, and PoorG = species of other poor grasslands; Axis length is 3.45 for axis 1 and 2.31 for axis 2. A representation with species and single plots can be found in Figure A3 in the Supplement.

Abbildung 2.4: DCA aller Aufnahmen in 1986 und 2018, basierend auf Präsenz/Absenz-Daten. Rote Umrisse umfassen alle Aufnahmen von Borstgrasasen und blaue Umrisse umfassen alle Aufnahmen von Feuchtheiden. Dabei stellen durchgängige Linien die Aufnahmen von 1986 dar und gestrichelte Linien die Aufnahmen von 2018. Dargestellte Umweltvariablen sind signifikant mit einer der beiden DCA-Achsen korreliert ($p <$ 0,05), mit R^2 $\geq$ 0,15. mF, mR, mN: Präsenz/Absenz-basierte Ellenberg-Zahlen für Bodenfeuchte, Bodenreaktion und Nährstoffe; Artenzahl (Number) und Deckungssummen (cover) der Artengruppen: NardG = Charakterarten der Borstgrasrasen, WetH = Charakterarten der Feuchtheiden, SSF = Charakterarten der Kleinseggenriede, AgriG = Arten des Wirtschaftsgrünlands, PoorG = Arten anderer nährstoffarmer Wiesen. Achsenlänge ist 3,45 für Achse 1 und 2,31 für Achse 2. Eine Darstellung mit Arten und einzelnen Plots findet sich in Abb. A3 im Anhang.

2.4 Discussion

Our results indicate an overall trend of pH recovery, but different levels of vegetation response between *Nardus* grasslands and wet heaths.

2.4.1 Soil reaction recovery

The results confirm the expected rise in pH values, as previously reported by Kirk et al. (2010), McGovern et al. (2011), Mitchell et al. (2018) (all UK) and Peppler-Lisbach et al. (2020) from central Germany. It is commonly thought that this is the effect of strongly reduced SO_2 emissions since the 1990s. Tipping et al. (2021) assume that pH recovery largely contributed to recent increases in plant species richness in the UK. This process apparently completely overrides the simultaneous further acidification through ammonium deposition.

Fifty years after the peak of SO_2 emissions (McGovern et al. 2011; Mitchell et al. 2018), this is an exciting opportunity to observe the rates of recovery from acidification, which are not yet well known (Kirk et al. 2010). In acid soils as surveyed in this study, silicate mineral weathering is the main acid-buffering process. It is considered to be a slowly operating buffering system (Kirk et al. 2010; Scheffer & Schachtschabel 2010). A pH increase of 0.75 on average, equivalent to an 82 % reduction in H^+-concentrations over 32 years, is therefore unexpectedly strong. However, weathering rates increase logarithmically with declining pH values (Scheffer & Schachtschabel 2010). This may offer an explanation as to why soils with initially lower pH values show larger increases in pH. Our findings confirm the results of a *Nardus* grassland resurvey study in continental Germany, which also found stronger pH increases in initially more acid soils (Peppler-Lisbach et al. 2020).

2.4.2 Changes in soil moisture and temperature

The observed increase in soil moisture as reflected in the mF values can be explained by clogged ditches in the context of nature conservation projects in the area (BioStation 2018). Precipitation changes, in contrast, cannot be hold as an explanation for increased soil moisture, as yearly precipitation has slightly decreased since the initial survey (DWD CDC 2018).

The observed significant rise in mT values might be a first manifestation of rising temperatures due to anthropogenic climate change. Indeed, mean annual temperatures in the survey period 1986–2018 were 1 °C higher than in the preceding 40 years (DWD CDC 2018). However, a more likely explanation is that the increase in mean mT values is influenced both by the reduction of cold-indicating species, which are nearly exclusively mosses, and by an increase in species with higher mT values that are mainly species of agricultural grasslands. When only vascular species are included in the calculation of mT, the increase remains significant although less pronounced (mean change of mT, vascular plants: 0.08). The increase or decrease of these species groups is likely determined by factors other than climate change, e.g. nutrient levels or poor detectability of mosses due to very dry weather.

2.4.3 Vegetation changes

Changes in *Nardus* grasslands

Although the sampled *Nardus* grasslands are exposed to general regional and global drivers like climate change, pH recovery, and nitrogen deposition in the range of critical loads, the vegetation response of these *Nardus* grasslands was not very pronounced. The observed changes were rather quantitative than qualitative – mR and mN values only increased significantly when weighted with cover values of species. In contrast to findings by Dupré et al. (2010) and Peppler-Lisbach et al. (2020), *Nardetalia* character species only decreased in cover, not in numbers. The rise in vascular plant species richness can be explained by the decline in Al-toxicity following pH recovery (De Graaf et al. 2009). Conditions have become suitable for a larger species pool, now also including acid-sensitive species that are mainly present in agricultural grasslands. However, these newly appearing species have not gained any dominance.

Evenness has slightly increased. There are no signs of competitive species like graminoids or tall herbs outcompeting small forbs (as in Dupré et al. 2010; Maskell et al. 2010; McGovern et al. 2011). On the contrary, low-competitive plants like the hemiparasitic *Rhinanthus minor* and *Pedicularis sylvatica* have profited, along with several small sedge species. *Molinia caerulea* and *Nardus stricta*, as fallow indicators, were pushed back. All these findings can be attributed to the resumption of regular management after the fallow phase preceding the initial survey. The annual mowing reduced the advantage of competitive species, and therefore led to a more homogeneous vegetation structure (Figure 2.5). Increased N-availability may be a reason for the decline of moss species (Lee & Caporn 1998; Carroll et al. 2003). At the same time, the summer of 2018 was exceptionally hot and dry, probably causing a temporary decline and poor detectability of bryophyte species.

The lack of strong eutrophication signs in *Nardus* grasslands were possibly caused by a removal of excess nitrogen by mowing or a limitation of other nutrients, especially phosphorous (P) or potassium (K). Mowing has been found to quickly decrease K levels (Mládková et al. 2015), while Verhoeven et al. (1993) reported a complete withdrawal of deposited nutrients by yearly mowing of grassland on fen soils in the Netherlands. Other studies estimate nitrogen removal by mowing to amount to 25–50 kg N ha^{-1} a^{-1} for Eifel grasslands (Schumacher et al. 2013), 41 kg N ha^{-1} a^{-1} in continental mountainous grasslands (Mládková et al. 2015) or 24–63 kg N ha^{-1} a^{-1} in coastal prairie grasslands (Maron & Jefferies 2001). All these values exceed the current N input by atmospheric deposition (approx. 11–12 kg N ha^{-1} a^{-1}, UBA (2021)). Schumacher et al. (2013) hypothesised this to be a major cause for continuously high alpha diversity in managed semi-natural grasslands of the Eifel mountains.

Additionally, the low measured ortho-phosphate concentrations suggest a phosphorus limitation. Phosphorus concentrations in 1986 and 2018 cannot be compared directly, due to differing soil-water extraction methods. The reported decrease is nevertheless plausible, also due to the fact that the centrifuged equilibrium soil solution used in 2018 would rather have contained more dissolved ions than the soil water used in 1986. As shown in fertilising experiments, phosphorus limitation can inhibit the uptake of additional nitrogen (Phoenix et al. 2003), as well as reduce eutrophication effects, including loss of species (Chytrý et al. 2009). To further investigate the nature of nutrient limitation, the plant tissue N:P ratio could be used (Koerselman & Meuleman 1996). This type of analysis was beyond the scope of the present study.

Another important factor affecting the change in vegetation composition is the availability of source populations of species that might be able to invade the present swards (Zobel et al. 2000; Foster 2001). The meadows studied are mostly surrounded by coniferous forest and thus isolated, not only from each other, but also from other types of grassland. A lack of propagule availability might also explain why more nutrient-demanding species are slow to colonise the swards, as opposed e.g. to the Rhön mountains, where *Nardus* swards are mostly embedded in agricultural grassland areas.

In summary, the mechanism most likely affecting vegetation response is the management regime, which requires annual mowing in summer, counteracting eutrophication and the dominance of single species. However, the current type of management might not be optimal for all typical *Nardus* grassland species. Especially *Arnica montana*, as a flagship-species of montane meadows, displays significant losses in frequency and cover, most likely due to a lack of open soil structures for generative reproduction (Figure 2.6) (Kahmen & Poschlod 1998; Richter 2014). Moreover, the extremely dry season of 2018 might have contributed to the decreased frequency and cover of *Arnica*, which is known to be very drought sensitive (Stanik et al. 2020).

Changes in wet heaths

Although overall conditions, such as pH recovery, atmospheric depositions, and climate change, affect the sites of wet heaths in the same way as the *Nardus* grasslands, evidences of eutrophication in vegetation change were much more pronounced in the wet heath sites. This is reflected by significant increases in mR and mN indicator values. The former wet heaths have transformed into wet variants of *Nardus* grasslands, small sedge-dominated swards or wet meadows with signs of eutrophication (e.g. presence of *Angelica sylvestris* and *Galium mollugo* agg.) (Figure 2.7). This agrees well with findings by Britton et al. (2017) from Scottish wet heaths.

The conditions of wet heaths were more acidic and nutrient-poor in 1986 than those of the *Nardus* grasslands, even after a 30-year fallow period preceding the initial survey. The historical land use practices that facilitated the formation of heaths, in this case the so-called “Schiffelwirtschaft” (Ludwig 1987; BfN 2017) consisted of a shorter arable phase, prepared by sod-cutting and burning to use the ash for fertilisation, and a longer fallow phase, with grazing and litter harvesting (Becker 1970). Therefore, the heaths established on very poor, undeveloped soils. Additionally, the dominant dwarf shrub species, especially *Erica tetralix* and to a lesser extent *Calluna vulgaris*, may have further acidified the soil by their use of ammonium as a nitrogen source (Berendse 1998). They serve as net accumulators of humus, as their litter has a high lignin content and decomposes only slowly (Leuschner & Ellenberg 2017b). Thus, after a fallow period of more than 30 years, a considerable humus layer had developed until 1986 (Ludwig 1987, Tab. 12). The start of annual mowing since the late 1980s disadvantaged and pushed back the dwarf shrubs as they are less able to compensate for annual biomass losses than the more regenerative grasses (Leuschner & Ellenberg 2017a). Once humus accumulation halted, decomposition could begin, leading to elevated nutrient availability (Berendse et al. 1987). Increased pH values and higher temperatures may have additionally enhanced the rate of humus decomposition (Leuschner & Ellenberg 2017a; Peppler-Lisbach & Könitz 2017). The atmospheric inputs of nitrogen may have additionally given grasses a competitive advantage over dwarf shrub species (Berendse et al. 1987).

Another key species for nutrient cycling is *Molinia caerulea*, which is able to withhold nutrients from the community by internal nutrient cycling (Berendse et al. 1987). The observed reduction in cover values of *Molinia* due to regular and early mowing could have led to increased nutrient availability for other species. Considering this background, the question arises, if annual mowing is a suitable management tool for preserving wet heath vegetation at all. More appropriate ways of managing and preserving the typical species composition of wet heaths are probably extensive grazing by sheep and occasional sod cutting.

2.4.4 Drivers of change

Differences between sites and initial syntaxon identity accounted for most of the explained variance in the dataset. The differences between sites translated to local conditions such as changes in water regime, fragmentation, or the behaviour of single land users. Differences between syntaxa represent the differing internal mechanisms that drive the responses of grasslands and heaths to annual mowing. Additionally, idiosyncrasies of single plots (e.g. plot-specific management history, disturbance events or pseudo-turnover) might have contributed to floristic turnover, but were not explicitly quantified. Obviously, changes in species composition were relatively poorly determined by the environmental factors investigated in this study, similar to findings reported by Peppler-Lisbach & Könitz (2017).

Figure 2.5: a) *Nardus* grassland (*Juncenion squarrosi* and *Galium saxatile-Nardus* community) in the “Mäusenest” area in the nature reserve “Baasemer Heide” near Berk. Photo: G. Ludwig, July 1986. b) Same view of “Mäusenest” in the nature reserve “Baasemer Heide” in 2018. *Nardus* grassland (*Juncenion squarrosi*) with transitions to small sedge swards (*Caricetum nigrae* Br.-Bl. 1915). Photo: L. Mazalla, 15.06.2018.

Abbildung 2.5: a) Borstgrasrasen (*Juncenion squarrosi* und *Galium saxatile-Nardus*-Gesellschaft) im „Mäusenest” im NSG „Baasemer Heide” bei Berk. Foto: G., Ludwig, Juli 1986. b) Gleiche Ansicht des „Mäusenests” im NSG „Baasemer Heide” in 2018. Borstgrasrasen (*Juncenion squarrosi*) mit Übergängen zu Kleinseggenrieden (*Caricetum nigrae* Br.-Bl. 1915). Foto: L. Mazalla, 15.06.2018.

Figure 2.6: a) *Nardus* grassland (*Juncenion squarrosi*) with *Arnica* flowering aspect. “Westlich Ehrend” in the nature reserve “Baasemer Heide” near Baasem. In the 2000s, this population was considered the largest in the NRW-part of the Eifel (Schumacher et al. 2007). Photo: G. Ludwig, June 1987. b) Same view of “Westlich Ehrend” in the nature reserve “Basemer Heide” in 2018. *Nardus* grassland (*Juncenion squarrosi*) also at the end of the blossoming time of *Arnica*. Photo: L. Mazalla, 24.06.2018.

Abbildung 2.6: a) Arnica-Aspekt des Borstgrasrasens (*Juncenion squarrosi*) „Westlich Ehrend” im NSG „Baasemer Heide” bei Baasem. In den 2000er Jahren wurde dieses Vorkommen als das größte im NRW-Teil der Eifel angesehen (Schumacher et al. 2007). Foto: G. Ludwig, Juni 1987. b) Gleiche Fläche in 2018 zum Ende der Blütezeit von Arnica, die aber kaum noch vorhanden war. Foto: L. Mazalla, 24.06.2018.

Figure 2.7: a) Wet heath (*Ericion tetralicis*). Nature reserve “Rinner Heide” near Sötenich. Photo; G. Ludwig, July 1985. b) Same view of nature reserve “Rinner Heide” near Sötenich in 2018. Eutrophic wet heath (*Ericion tetralicis*) with nutrient indicators (e.g., *Galium mollugo* agg., *Angelica sylvestris*). Photo: L. Mazalla, 20.06.2018.

Abbildung 2.7: a) Feuchtheide (*Ericion tetralicis*). NSG „Rinner Heide” bei Sötenich. Foto: G. Ludwig, Juli 1985. b) Gleiche Ansicht des NSG „Rinner Heide” bei Sötenich in 2018. Eutrophierte Feuchtheide (*Ericion tetralicis*) mit Nährstoffzeigern (z.B. *Galium mollugo* agg., *Angelica sylvestris*). Foto: L. Mazalla, 20.06.2018.

The influence of the drivers did not differ systematically in terms of strength or direction between wet heaths and *Nardus* grasslands. The increase in pH values between 1986 and 2018 did show the hypothesised influence on variables like total vascular species richness, number of agricultural grassland species, and cover of *Nardetalia* character species; its overall effect was, however, limited, as indicated by low proportions of explained variance in regression models and RDA. We conclude that even though pH recovery clearly drives some of the change, as previously reported by Roem & Berendse (2000), Dupré et al. (2010) and Peppler-

Lisbach et al. (2020), it was not the main driver of overall vegetation change. It was not possible to directly test the influence of atmospheric deposition, due to the limited spatial extent of the study with relatively uniform deposition rates over all sites. The typical effects of elevated N deposition are, however, well described in the literature. As these are only moderately represented here, we assume that nitrogen deposition is also not the most crucial driver of vegetation change.

In sum, we think that the initial community type (and the conditions that shaped it), together with the reintroduction of management after 1986, and other local factors, mainly determined the changes that occurred since then. Studies from forests also found that management legacies dictate floristic community responses to global drivers like deposition and climate change (Perring et al. 2018).

2.4.5 Pseudo-turnover

Observer and location bias are sources of uncertainty in all resurvey studies (Kapfer et al. 2017). However, due to careful study design, we consider it very unlikely that the consistent directional trends uncovered in the present study should have been decisively influenced by pseudo-turnover. We are confident that the general patterns and trends reflect the true development of vegetation composition in these grasslands and heaths.

2.5 Conclusions

Since the original survey in 1986, we found the expected increase in soil pH, presumably due to the reduction of sulphur dioxide emissions. It is likely that the appearance of several acid-sensitive species can be attributed to the effects of increased pH, i.e. decreased aluminium or ammonium toxicity and increased nutrient supply due to increased remineralisation. The anticipated eutrophication was especially pronounced in the wet heath sites that had transformed into more mesotrophic vegetation types. In *Nardus* grasslands, however, species composition shifts towards eutrophication were relatively weak. This result was somewhat unexpected, especially compared to other studies from German *Nardus* grasslands, where even less pronounced increases in pH were linked to more distinct indications of eutrophication. We conclude that the regular management applied to the sites contributed essentially to this outcome by counteracting eutrophication in an effective way. In the surveyed *Nardus* grasslands, the relatively early date of mowing (from mid-July) enabled a successful removal of nutrients and resulted in a characteristic structure and species composition. However, some quantitative changes (increase in cover-weighted mR and mN, decrease in cover of character species) indicate a certain risk of eutrophication and loss of specialist species, and that continuing management will be crucial for a sustained conservation of *Nardus* grasslands. The same management, however, was not able to preserve wet heaths equivalently. By strongly disadvantaging the dominant dwarf shrubs, regular mowing altered the internal nutrient cycling of the heaths which led to increased eutrophication effects. Other management strategies, e.g. periodic top soil removal, possibly combined with extensive grazing, should be considered for maintaining the wet heath stands. In any case, we recommend further monitoring, preferably every five years, to calibrate management plans to secure the survival of these important remnants of historical land use.

2.6 Erweiterte deutsche Zusammenfassung

Einleitung – Halbnatürliche Offenlandvegetation ist in Europa ein Hotspot der Biodiversität (Habel u. a. 2013; Dengler u. a. 2014). Von der jüngeren Vergangenheit bis in die Gegenwart stellen Landnutzungsveränderungen, atmosphärische Depositionen, insbesondere von reaktivem Stickstoff und Schwefeldioxid, und neuerdings auch der Klimawandel eine Gefahr für die Artenvielfalt dieser Habitate dar (Sala u. a. 2000; Poschlod u. a. 2005). Die vorliegende Wiederholungsuntersuchung der Vegetation von Borstgrasrasen, Pflanzengesellschaft des Jahres 2020 (Schwabe u. a. 2019), und Feuchtheiden in der Eifel zwischen 1986 und 2018 hatte zum Ziel, die Entwicklung dieser Vegetationstypen unter dem Einfluss der genannten Stressoren zu untersuchen. Die Landnutzung der Untersuchungsflächen bestand im Untersuchungszeitraum aus einem Pflegemanagement durch den Vertragsnaturschutz; bis kurz vor der Erstaufnahme hatten die Flächen längere Zeit brach gelegen. Gemäß diesen Rahmenbedingungen erwarteten wir daher, dass (i) das Pflegemanagement mit einschüriger Mahd die Vegetationstypen zumindest erhalten konnte, (ii) der pH-Wert des Bodens durch den Rückgang der Schwefeldioxid-Emissionen seit den 1980er Jahren wieder angestiegen ist, und (iii) dieser pH-Anstieg in Kombination mit Stickstoff-Emissionen zu einer Eutrophierung der Standorte mit entsprechenden Veränderungen der Artenzusammensetzung geführt hat.

Material und Methoden – Die Studie basiert auf Aufnahmen von Gerhard Ludwig aus dem Jahre 1986 (Ludwig 1987). Die untersuchten Borstgrasrasen und Feuchtheiden befinden sich in der Nord-Eifel, ca. 50 km südwestlich Bonn. Bis kurz vor der Erstaufnahme hatten die Flächen ca. 30 Jahre lang brach gelegen. Seitdem wurden sie im Rahmen von Vertragsnaturschutzprogrammen jährlich einmal ab Mitte Juli gemäht. Im Jahre 2018 wurden dann in neun Gebieten 50 Vegetationsaufnahmen von Borstgrasrasen und 14 von Feuchtheiden wiederholt und in allen Aufnahmeflächen der pH-Wert, in 22 Flächen auch der Phosphat-Gehalt des Bodens gemessen. Aus der Artenkombination der Aufnahmen wurden mittlere T-, F-, R- und N-Zeigerwerte nach Ellenberg berechnet. Ferner diente die Stetigkeit und Deckung der Arten von sechs syntaxonomisch-ökologischen Artengruppen als abhängige Variablen; diese Artengruppen beinhalteten die Charakterarten der (1) Borstgrasrasen, (2) Feuchtheiden, (3) Kleinseggenriede und des (4) Wirtschaftsgrünlands sowie (5) weitere Arten der Magerwiesen und (6) Brachezeiger. Weiterhin wurden die Veränderung der Artenzahl, Evenness, Artenzugewinne und -verluste, das Verhältnis von Gräsern i. w. S.

und Kräutern, die Deckung von Zwergsträuchern sowie ein Bracheindex der Vegetation untersucht. Signifikante Unterschiede in der Häufigkeit und Abundanz von einzelnen Arten wurden ebenfalls ermittelt. Um den Effekt der Faktoren pH_{1986}, Veränderung des pH, $Bracheindex_{1986}$, Gebiet und Syntaxon auf die Vegetationsveränderungen zu untersuchen, wurden multiple lineare Modelle und eine RDA erstellt.

Ergebnisse – Die pH-Werte stiegen zwischen 1986 und 2018 im Mittel von 3,9 auf 4,6 an. Die Ellenberg-Zeigerwerte für Bodenreaktion und Nährstoffe stiegen lediglich in den Feuchtheiden signifikant an, während sie in den Borstgrasrasen stabil blieben (Abb. 2.1). Die mittlere Artenzahlen pro Aufnahme blieb in den Borstgrasrasen unverändert, erhöhte sich dagegen in den Feuchtheiden signifikant. Die Evenness und das Verhältnis von Gräsern zu Kräutern veränderten sich nicht signifikant (Abb. 2.2). Alle 1986 vorhandenen Borstgrasrasen konnten, mit hohen Gesamt-Artenzahlen (Mittel von 34,3 Arten pro 20 m^2) und einem Anteil von 40 % Nardetalia-Charakterarten, auch 2018 noch als solche angesprochen werden. Die Deckungssumme der Charakterarten der Borstgrasrasen ging allerdings zurück, während die Anzahl der Arten des Wirtschaftsgrünlands und der Kleinseggenriede zunahmen (Abb. 2.3, Abb. A2). Wohl als Ergebnis der regelmäßigen Mahd profitierten konkurrenzschwache Arten (z.B. *Carex pilulifera*, *Pedicularis sylvatica*), während Arten, die bei Brache zur Dominanz gelangen können (insb. *Molinia caerulea*), zurückgedrängt wurden. In den Feuchtheiden waren die Veränderungen insgesamt deutlich stärker; die Bestände haben sich zu feuchten Varianten von Borstgrasrasen, von Kleinseggen dominierten Rasen oder Feuchtwiesen entwickelt. Die Charakterarten der Feuchtheiden (z.B. *Erica tetralix*, *Trichophorum cespitosum* subsp. *germanicum*) nahmen stark ab und traten nur noch mit einem Anteil von 3 % an der Gesamt-Artenzahl auf. Auch die multivariate Analyse zeigt, dass sich die Feuchtheiden im Untersuchungszeitraum deutlich stärker verändert haben als die Borstgrasrasen (Abb. 2.4). Zudem sind sich die Feuchtheiden und Borstgrasrasen floristisch ähnlicher geworden. Gleichzeitig haben sich die Aufnahmewerte in der DCA in Richtung feuchterer und nährstoffreicherer Bedingungen verschoben. Die linearen Regressionsmodelle und die RDA zeigen, dass die Vegetationsveränderung in einem signifikanten Kontext mit der Veränderung des pH-Wertes und des Bracheindex im Jahr 1986 stand (Tab. 2.1, Tab. 2.2). Ein Großteil der Veränderungen hing laut Modellen jedoch vom Ausgangstyp der Bestände (Borstgrasrasen vs. Feuchtheiden) ab, d.h. die Vegetationstypen haben sich unterschiedlich entwickelt.

Diskussion – Der durchgängige Anstieg des pH-Werts kann auf den Rückgang der SO_2-Emissionen seit den 1980er Jahren zurückgeführt werden (Kirk u. a. 2010; Peppler-Lisbach u. a. 2020). Er hatte zwar die erwarteten Effekte auf die floristischen Veränderungen. wie z.B. einen positiven Einfluss auf Nährstoffzeiger und einen negativen auf Kennarten der Borstgrasrasen, trug allerdings in einem relativ geringen Umfang zur Veränderung der Vegetation bei. Dabei konnten Eutrophierungserscheinungen vor allem in den Feuchtheiden beobachtet werden, wohingegen die Borstgrasrasen stabiler waren. Diese relativ schwachen Veränderungen der Borstgrasrasen sind sehr wahrscheinlich ein Erfolg der regelmäßigen und nicht zu spät stattfindenden Mahd und den damit einhergehenden Austrägen von Stickstoff oder anderen Nährstoffen (v.a. Phosphor und Kalium) (Verhoeven u. a. 1993; Mládková u. a. 2015). Der Grund für die stärkeren Veränderungen in den Feuchtheiden liegt zum einen in der Reduktion der ursprünglich dominierenden Zwergsträucher aufgrund ihrer geringen Verträglichkeit gegenüber regelmäßiger Mahd (Leuschner & Ellenberg 2017b). Zum anderen konnte als Folge die maßgeblich durch die Zwergsträucher aufgebaute Rohhumus-Auflage zunehmend zersetzt werden, was zu einer erhöhten Nährstoffverfügbarkeit führte (Berendse u. a. 1987). Erhöhte pH-Werte (Peppler-Lisbach & Könitz 2017) und Temperaturen (Leuschner & Ellenberg 2017b) könnten die Geschwindigkeit des Humusabbaus zusätzlich gefördert haben. Zusammenfassend sind wir der Überzeugung, dass der Anstieg der pH-Werte und möglicherweise auch atmosphärische Stickstoff-Einträge nur eine Mitursache für die beobachteten Vegetationsveränderungen waren, während die wiedereingeführte und regelmäßig praktizierte Pflegemahd entscheidend war.

2.7 Acknowledgements

We would like to thank Wolfgang Schumacher (Mechernich) and Stefan Meisberger (Biologische Station Kreis Euskirchen, Nettersheim) for manifold information and support. English-language services were provided by stels-ol.de.

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— Chapter 3 —

Microclimate shapes vegetation response to drought in calcareous grasslands

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Applied Vegetation Science, 25(3): e12672.
https://doi.org/10.1111/avsc.12672

Ophrys apifera, a typical calcareous grasslands orchid.

Abstract

Questions: Semi-natural grasslands have been shown to be relatively resilient to drought events, but there seems to be no uniform response of different grassland types or across species. The typical vegetation of calcareous grasslands, which are biodiversity hotspots in Europe, reportedly even profits from droughts. What was the response of their vegetation, considering different species groups, to the recent periods of intense summer droughts? How did differences in microclimate, such as between steep, south-facing slopes (SSF) and flat or north-facing slopes (FNF), affect species composition and drought response?

Location: Semi-arid calcareous grasslands (*Mesobromion*) in North-West Germany.

Methods: In 2019, we resurveyed 112 vegetation plots from 25 sites first established in 2008, after 11 exceptionally dry years. Species identities and cover were assessed in plots of 1 m^2. We used linear mixed models to determine the effect of microclimate on species composition and drought response. Vegetation changes were visualised by a NMDS.

Results: In the initial survey in 2008, the species composition was significantly influenced by the microclimate, with positive effects of dry and warm conditions on SSF on character species. Phosphorus availability played an equally important, albeit contrasting, role. Vegetation change between 2008 and 2019 showed strong signs of the severe droughts. In contrast, dry conditions on FNF favoured an increase in total species richness and character species. However, eutrophication indicators increased here as well.

Conclusions: We conclude that sites with a dry and warm microclimate have so far had a positive, stabilising effect on the typical vegetation of calcareous grasslands. However, increasing droughts due to climate change pose a potential threat to the characteristic species composition, especially at sites with hot and dry microclimates.

Keywords *Brachypodium pinnatum*, *Bromus erectus*, Calcareous grasslands, Climate change, Drought, Dry grasslands, Microclimate, Resurvey study, Semi-natural grasslands, Topography

3.1 Introduction

Climate change as a driver of weather extremes is expected to become an increasingly important factor for biodiversity (Thuiller et al. 2005; Behrens et al. 2009; Pompe et al. 2011). Drought periods will most likely increase in frequency and intensity worldwide (IPCC 2014) and regionally (DWD 2018). Since 2015 to present, Europe has experienced the most severe summer droughts in over 2000 years (Büntgen et al. 2021). Although a direct causal link between single extreme weather events and anthropogenic climate change is impossible to prove, a recent review found numerous examples of detrimental effects of climate change on biodiversity (Pecl et al. 2017).

So far, there is no general agreement on the reaction of semi-natural grasslands to climate change. In experimental studies, they have proven relatively resilient to drought, both in terms of ecosystem processes and species composition (Grime et al. 2008; Bloor et al. 2010; Maalouf et al. 2012; Dengler et al. 2014; Fry et al. 2014). While productivity was commonly observed to decrease in response to drought, it recovered quickly after the end of the drought (Sternberg et al. 1999; Morecroft et al. 2004; Evans et al. 2011; Hoover et al. 2014). There appears to be no uniform response of different grassland types, or of different functional groups and individual (dominant) species, to the same treatment (Grime et al. 2000; Maalouf et al. 2012; Hoover et al. 2014).

We here conducted a resurvey study of semi-arid calcareous grasslands in North-West Germany after a decade of exceptional drought. Calcareous grasslands are hotspots of biodiversity in Europe and show a record-breaking plant species density (Wilson et al. 2012). Furthermore, a large proportion of the total German species pool (approx. 15 %) is restricted to calcareous grasslands (WallisDeVries et al. 2002; Dengler et al. 2014). Even though their great importance for biodiversity and dependence on permanent anthropogenic management put them in the focus of conservation planning (Poschlod & WallisDeVries 2002), calcareous grasslands are threatened in many ways. At present, area losses as a result of land use change are considered the greatest threat to these grasslands and their species (Sala et al. 2000; WallisDeVries et al. 2002; Pompe et al. 2011). In addition, they are negatively affected by habitat degradation due to eutrophication and lack of management (Bobbink & Willems 1987; Bennie et al. 2006; Diekmann et al. 2014; Bauer & Albrecht 2020; Ridding et al. 2020).

In calcareous grasslands, drought events are commonly considered to have mostly positive effects, although Petermann et al. (2007) attested them a high sensitivity to climate change, as their situation is already precarious due to the above-mentioned threats and low regeneration potential. Species of calcareous grasslands are the best adapted to drought and heat in the Central European landscape, and therefore likely to benefit from a warming climate through an increase in potential habitat area (Behrens et al. 2009; Pompe et al. 2011). Dry spells presumably contribute to the long-term stability of the typical species assemblage, because more competitive species, which are not adapted to these stressful conditions, are regularly “sorted out” (Bennie et al. 2006; Leuschner & Ellenberg 2017b; Fischer et al. 2020). Droughts may also mitigate the effects of eutrophication by limiting water availability and thus the competitive power of potentially invading species (Bennie et al. 2006). These positive effects can be extended to dry conditions, which are not caused by weather but by microclimatic conditions. Perring (1959) showed that topography-controlled wetness is an important factor for species composition in calcareous grasslands, with SSW exposed slopes being the driest, and NNE exposed slopes being the wettest. The impact of topography on local climatic conditions was also demonstrated by Suggitt et al. (2011), showing differences in maximum temperature of 7 °C, and occasionally up to 20 °C, between north- and south-facing slopes in heather moorland. In contrast, experimental studies in semi-arid calcareous grasslands found only minor effects of drought on species composition, despite a strong reduction in productivity (-35%) and a significant decrease in species numbers (Grime et al. 2008). Maalouf et al. (2012) found no effects of a two-year spring drought simulation on species richness or Shannon diversity in a mesic calcareous grassland, but significant reductions in a xeric grassland.

In the present resurvey, we investigated the effects of extreme drought on the species composition and richness of calcareous grasslands in North-West Germany. In doing so, we focused not only on differences between species groups with varying habitat requirements, but also between sites with different microclimatic conditions.

Our main hypotheses were: H1. Particularly warm and dry microclimates generally have a positive effect on the characteristic species composition of dry grasslands. To test this hypothesis, we used the data of the initial survey in 2008. H2. The species composition of semi-arid calcareous grasslands is generally robust to the exceptional droughts of the last decade. H3. Changes in species composition and richness between the two surveys as induced by drought depend on the microclimatic conditions of the site and differ between species groups.

3.2 Materials & Methods

3.2.1 Study area

The 25 study sites are located in Lower Saxony, Germany, between the latitudes of 51.507 and 52.152 and the longitudes of 9.570 and 10.044, except for one isolated site close to Osnabrück (52.209, 7.955), approximately 100 km further west. For a map showing the locations of the study sites, see Figure A4 in the Appendix. Sites were limited to areas with a suboceanic climate with mean temperatures of around 8.8 °C and mean yearly precipitation of approx. 700 mm (DWD 2021). The sites were selected as to represent the typical calcareous grassland vegetation in North-West Germany, being assigned to the alliance *Bromion erecti* Koch 1926 in the class *Festuco-Brometea* Br.-Bl. et Tx. in Br.-Bl. (1949). Soils are shallow with a median depth of 10 cm (min. 4 cm, max. 35 cm), while pH values range from 6.1 to 7.3, with a median of 7.1. According to model data from the study region, nitrogen deposition varied between 13 and 17 kg N ha^{-1} y^{-1}, with one outlier of 23 kg N ha^{-1} y^{-1} at one site (data from 2013–2015, UBA 2021). The environmental conditions would naturally support forest, mainly mull beech forests (*Galio odorati-Fagenion* Tx. 1955) on base-rich soils, some tending to mesic limestone beech forests (*Hordelymo-Fagetum* Kuhn 1937), some to moder beech forests on more acid soils (*Luzulo-Fagetum* Meusel 1937) (Suck et al. 2013; Leuschner & Ellenberg 2017a). The grasslands are kept open by human intervention. All sites represent nature reserves, 21 of them are additionally registered as Natura 2000 areas. In 2008, ten of the sites were mown, seven grazed and eight managed in a mixed form with grazing in summer and a regular additional cut in autumn or winter. In 2019, four of the mown sites had been converted to grazing (2) or a mixed mowing/grazing regime (2), with the management of all others remaining unchanged.

There were only 11 years between initial and resurvey study. However, these years were exceptionally dry: According to the soil moisture index (SMI), published by the drought monitor for Germany (Zink et al. 2016), none of these 11 years reached the long-term median of growing season SMI of all years between 1951 and 2008. The first survey in 2008 was done after a period of relatively stable growing season SMI since the middle of the 1990s, except for the drought year 2003 (Figure 3.1). The second survey year 2019 was the seventh driest year on record and followed a period of significantly reduced SMI (Wilcoxon rank test of SMI in 2008–2019 against the years 1951–2007, $p = 0.002$).

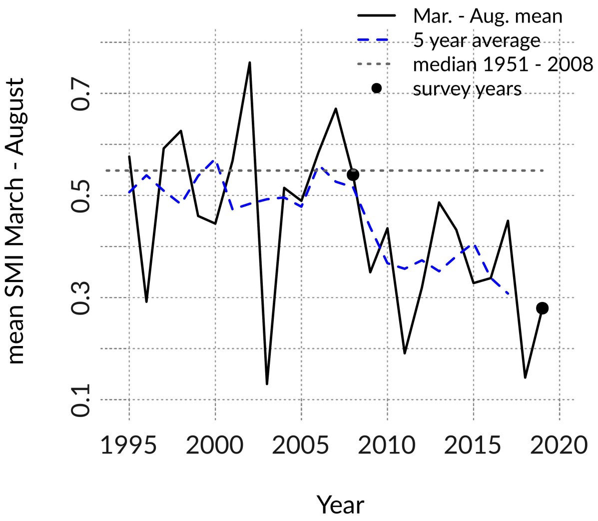

Figure 3.1: Mean soil moisture index (SMI) during the growing season (March–August) from 1995 to 2019.

3.2.2 Data sampling

The resurvey is based on 125 plots of 1 m^2, five in each of the 25 sites, sampled from late May to July 2008 in the context of a European project on atmospheric nitrogen deposition and vegetation change (e.g. Dupré et al. 2010). The five plots per site were positioned in a stratified random approach, ensuring to capture the variation in environmental conditions but at the same time randomly laying out the plots in the different site types. In most cases the plots were well spaced within a site, only rarely plots were located close to each other when the grassland site was small and environmental variation was strong on a small spatial scale. A full list of vascular plants and their cover was compiled. GPS data for the position of each plot was recorded. Eight of the original plots had obviously incorrect (e.g. located in adjacent arable fields) or missing GPS data. Due to time or weather constraints, five other relevés could not be resurveyed. This left a total of 112 resampled relevés (from 15 sites with five plots each, nine sites with four plots each and one site with two plots), surveyed in June and July of 2019. As the GPS coordinates were not sufficiently exact to allow us a precise relocation, areas with small-scale heterogeneity or more overgrown with shrubs than average for the site were avoided in the resampling to obtain homogeneous plots. This corresponds to the methodology of plot selection in the original study. Species cover values were estimated with a modified Domin scale in both sampling periods. Soil and topographic data were collected for all plots in 2008. These variables included: soil depth (mean of five measurements done with a metal pin), inclination and aspect of the slope, C/N-ratio, soil phosphorus concentration (Olsen extraction), and soil pH measured in $CaCl_2$ solution. Field capacity was extracted from soil maps (LBEG 2021), representing the amount of water a soil is able to hold when it is saturated with water.

3.2.3 Data analysis

All data was organised with Turboveg (Hennekens & Schaminée 2001) and analyses were conducted with R (R Core Team 2020) and RStudio (RStudio Team 2016), including the packages exactRankTests (Hothorn & Hornik 2019), ggeffects (Lüdecke 2018), lmerTest (Kuznetsova et al. 2017), ncdf4 (Pierce 2019), r2glmm (Jaeger 2017), reshape2 (Wickham 2007), scales (Wickham & Seidel 2019), vegan (Oksanen et al. 2019), vegdata (Jansen & Dengler 2010), viridis (Garnier 2018), and zoo (Zeileis & Grothendieck 2005). Species names were harmonised according to the GermanSL1.3 (Jansen & Dengler 2008).

To characterise the sites in terms of temperature and water availability, a heat index integrating the effects of slope inclination and aspect was calculated (Parker 1988):

$$heatindex = cos(aspect - 225) \cdot tan(inclination)$$

Steep slopes facing south-west obtain the highest scores, while steep slopes facing north-east have the lowest, negative, values. Plane sites by definition have a score of 0. Heat indices varied between -0.35 and 0.70 in our dataset. Bennie et al. (2006) classified slopes into three categories, which we merged into two groups for presentation purposes. Steep/south-facing slopes were accordingly defined to have an inclination of >15° and are facing SE to W, while flat/north-facing slopes either have inclinations <15° or are facing NW to E. The category "steep and south-facing" corresponds to heat indices of 0.27 or more.

Mean weighted Ellenberg indicator values (Ellenberg et al. 1992) for light (mL), soil moisture (mF) and nutrients (mN) were calculated for each site, based on square-root transformed species cover values. Evenness was calculated as a measure for the dominance structure of the stands (Pielou 1966). We also computed pairwise Sørensen dissimilarities of all plots between 2008 and 2019 based on cover values of all species (Borcard et al. 2018). The grasses-to-forbs ratio was calculated by dividing the cumulative cover of all graminoid species (including *Poaceae, Cyperaceae* and *Juncaceae*) by the sum of cover of all non-graminoid herbaceous species (dicotyledons and monocotyledons).

All species were classified as belonging to one of six plant sociological groups, following Ellenberg et al. (1992). 1. Dry grassland character species of *Festuco-Brometea* and *Koelerio-Corynephoretea*, n = 39; 2. Other species of nutrient-poor grasslands, including character species of *Calluno-Ulicetea* and *Molinio-Arrhenatheretea* with Ellenberg N values ≤ 3, n = 24; 3. Agricultural grassland species: Character species of *Molinio-Arrhenatheretea* with Ellenberg N values > 3, n = 31; 4. Ruderal species: character species of *Sisymbrietea*, *Stellarietea mediae*, *Artemisietea vulgaris*, *Galio-Urticetea* and *Agrostietea stoloniferae*, n = 24; 5. Fallow indicators: character species of coniferous and broad-leaved forests as well as of communities of forest edges and clearings, n = 55; 6. Indifferent species (n = 37).

In order to test which variables had an effect on the species composition in the first survey year (2008), linear mixed models for several vegetation indices were generated with automatic backwards selection. The 25 study sites were defined as a random factor to eliminate their individual differences before analyses and therefore account for the block design of the study. Dependent variables were total species number per plot, proportions of abundance and cover of the five species groups, mN, mF, and mL, the grasses-to-forbs ratio, and evenness. Predictor variables were soil chemical parameters (phosphorus, pH, C/N), topographic conditions (inclination, heat index, soil depth, field capacity), and management type (factor variable: mown, grazed, grazed/mown). Heat index and inclination were positively correlated ($p < 0.001$, Kendall's $\tau = 0.51$), but still sufficiently independent to be used in the same model to test for independent effects of heat index and topography alone. Relevant interaction terms were included. Only the 2008 data were used for these models to avoid confounding effects of drought. All models were checked for normality of residuals and heteroscedasticity. Dependent variables of models whose residuals did not follow a normal distribution were rank-transformed (cover of agricultural grassland species, mF, grasses-to-forbs ratio, evenness). R^2 values were calculated with the standardized generalized variance approach (function r2beta in Jaeger (2017)).

Differences (Δ) between 2008 and 2019 of the vegetation indices listed above were calculated as follows:

$$\Delta Var = Var2019 - Var2008.$$

To test for differences in the means of these indices between 2008 and 2019, a Wilcoxon signed rank test was performed. The significance of overall vegetation change between 2008 and 2019 was tested by a permutational Manova based on cover-weighted Sørensen dissimilarites (function “adonis” from Oksanen et al. 2019). Differences in multivariate dispersion of the years 2008 and 2019 were tested with the function “betadisper”.

To examine whether changes in species composition between 2008 and 2019 differ between sites with different microclimatic conditions, another set of linear mixed models was constructed. Changes (ΔVar) in the above-mentioned vegetation indices were used as dependent variables here. A categorical variable with the two levels “steep and south-facing slopes” and “flat or north-facing slopes” as adapted from Bennie et al. (2006) was used as predictor. Study site again served as a random factor. For each dependent ΔVar, their respective baseline values (Var2008) were additionally entered into the model to correct for the artefact of the so-called “regression to the mean” (EMA 2015; Mazalla & Diekmann 2022). This phenomenon describes the tendency of change scores to be negatively related to their baseline values. Since the baseline values of most variables are already correlated with the predictor variable (e.g. there were lower species numbers on steep, south-facing slopes in 2008), regression to the mean might interfere with the effect of independent variables on the observed change. It is therefore crucial to correct for this artefact (Mazalla & Diekmann 2022). We are aware that the model coefficients for the respective baseline variables are ecologically uninterpretable, as they are correlated with the error terms, and we will therefore not discuss them. The outcomes of these models are graphically displayed as boxplots, showing the predicted model values for the two categories “steep and south-facing slopes” and “flat or north-facing slopes”, while fixing the effect of the baseline value at its mean value and averaging over all sites (function ggeffect from Lüdecke (2018)).

To visualise vegetation change, an NMDS ordination was performed based on Sørensen distances of square-root transformed cover data of all species in both survey years, using the metaMDS function from Oksanen et al. (2019). For the reduction to two dimensions, stress was 0.25.

3.3 Results

3.3.1 Influence of microclimate on species composition in the initial survey

Both heat index and soil phosphorus (P) had significant effects on the species composition in 2008 (Table 3.1). As was to be expected, P had a positive influence on more nutrient-demanding species (species of agricultural grasslands), and also on mN and mF. At the same time, the proportion of dry grassland character species and other species of nutrient-poor grasslands was lower at higher P levels. Heat index and inclination affected the species composition in the opposite direction: the steeper and more sun-exposed the plot was, the more dry grassland character species and fewer agricultural grassland species were present. Similarly, mF and mN were lower at higher heat indices, while mL increased at greater inclinations. Soil depth, field capacity, C/N ratio and management rarely had significant effects. However, soil depth and C/N often appeared in interaction terms, with inclination or heat index being less relevant when soil depth or C/N ratio were high. The form of land use was only important for the share of poor grassland species, with this being highest for grazing only, intermediate for mowing and lowest for a mixture of both methods. Soil pH did not have any significant influence on the vegetation. The models for total species richness, percentage of ruderal species and the grasses-to-forbs ratio showed no significant drivers among any of the available predictor variables. In the case of total species richness, 56 % of variance was explained by the identity of the site as a random factor. The latter generally explained a high amount of variance in all models, with values ranging from 13 % to 67 % (mean 44 %). The model for the proportion of dry grassland character species is presented in more detail as an example (Figure 3.2). The proportion of specialist species is positively influenced by the heat index (slope of the fitted model) and negatively by P (parallel lines of the fitted model). However, the heat index becomes less important when soil depth increases (from left to right panel). Therefore, the slope of the model estimates becomes increasingly flat and eventually nearly zero at a soil depth of 15 cm.

Table 3.1: Summary of mixed linear models for vegetation variables in 2008. +: significantly positive, −: significantly negative effect of the predictor (columns) on the dependent variable (rows). mL, mF, mN: mean Ellenberg indicator values for light, soil moisture, and nutrients. P: soil phosphorus content. C/N: soil carbon to nitrogen ratio. % site variation: share of variance explained by the site as the random factor. For full table with estimates see Table A9 in the Appendix.

	R^2	heat index	incli-nation	P	soil depth	field capacity	C/N	land use	heat index: soil depth	incli-nation: soil depth	soil depth: field capacity	heat index: C/N	% site varia-tion
dry grasslands character species													
% species	0.26	+	.	−	.	.	.	.	−	.	.	.	48%
% cover	0.31	+	.	−	.	.	+	.	.	.	.	.	66%
agricultural grassland species													
% species	0.37	−	−	+	.	.	.	.	.	.	.	+	13%
% cover	0.39	−	−	+	.	.	−	.	.	+	.	+	32%
other poor grassland species													
% species	0.30	.	+	−	+	+	.	+/−	.	.	−	.	19%
other indices													
mL	0.14	.	+	.	.	.	.	.	.	−	.	.	56%
mF	0.30	−	.	+	.	.	.	.	.	.	.	+	67%
mN	0.50	−	−	+	−	−	.	.	.	+	+	+	44%
evenness	0.10	.	−	.	.	.	.	.	.	.	.	.	35%

In summary, indices reflecting typical calcareous grasslands were consistently higher at sites with steep, south-facing slopes (Figure 3.3). The proportion of dry grassland character species was on average high at all sites, but significantly higher on steep, south-facing slopes (mean 37 %) than on north-facing slopes or flat sites (mean 30 %). The absolute number of character species was also higher on extremely dry and hot sites (mean 7.2) compared to flat or north-facing slopes (mean 6.7) (not shown). The proportion of agricultural grassland species was lower on south-facing slopes (mean 10 %) than on north-facing slopes or flat sites

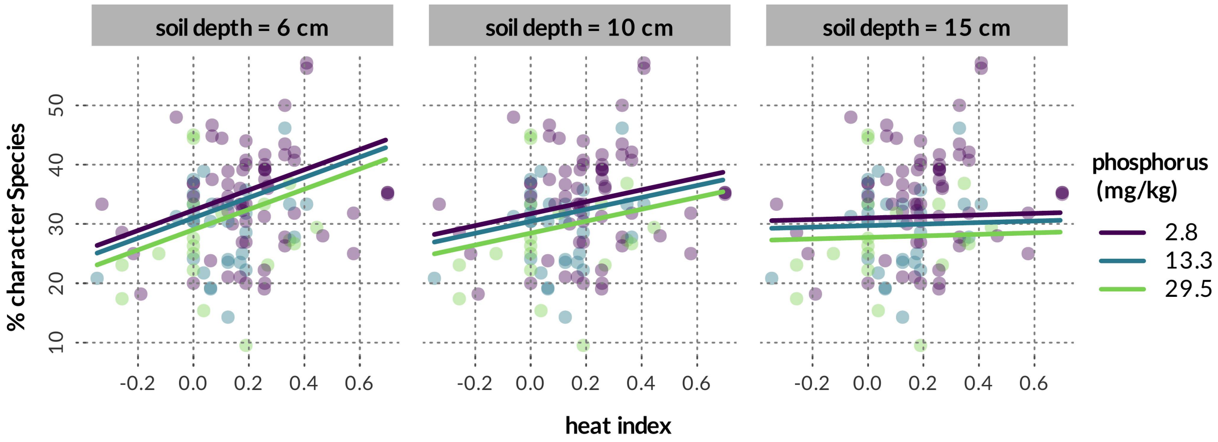

Figure 3.2: Proportion of dry grassland character species per plot in 2008 as a function of heat index, soil phosphorus and soil depth.

(mean 13 %). Accordingly, the consistently low mN value (between 3 and 3.5 in the majority of sites) was even lower on south-facing slopes. Overall species richness was significantly lower at the driest sites (mean 22.6 vs. 20.1).

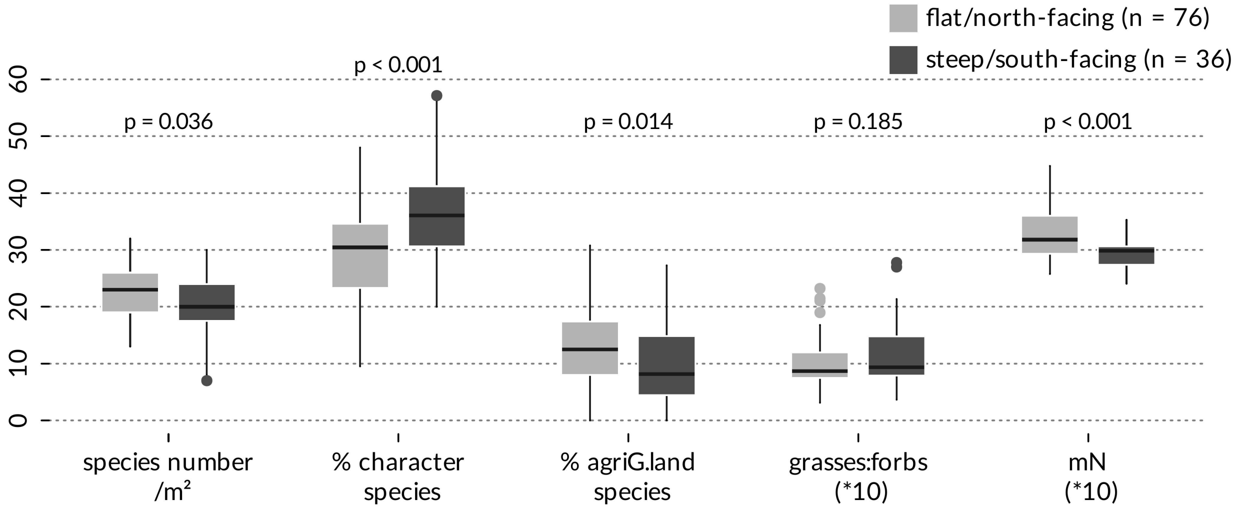

Figure 3.3: Comparison of vegetation parameters between steep, south-facing slopes and flat or north-facing slopes in 2008. For the grasses-to-forbs ratio, three extreme outliers were removed from the graph for better readability. p values were computed with a Wilcoxon signed rank test for unpaired data.

3.3.2 General vegetation change between 2008 and 2019

Impacts of the recent droughts are reflected in changes in the species composition between 2008 and 2019 (Table 3.2). The average number of species per plot increased only slightly, but the species composition changed significantly (Permanova: $R^2 = 0.04$, $p < 0.001$). However, dispersion was also significantly greater in 2019 than in 2008 ($p = 0.02$). The vegetation became sparser, as total cover decreased. Species groups that profited over the 11 resurvey years were the specialist species of dry grasslands, ruderal species, and fallow indicators.

Grassland species adapted to nutrient-poor conditions but not to drought decreased in number and proportion of cover, whereas agricultural grassland species decreased in cover only. Of the mean Ellenberg indicator values, only mF decreased, while mN and mL remained unchanged. The grasses-to-forbs ratio was significantly reduced, as was evenness. The latter was highly negatively correlated with the cover of *Bromus erectus* (Spearman's ρ = -0.57, $p < 0.001$). Where evenness decreased the most (lowest 25 % quantile: decrease greater than -0.09 %), also *B. erectus* had increased most, resulting in mean cover values of 41 % in 2019. While *B. erectus* was able to spread, *Brachypodium pinnatum* as the second potentially dominant grass suffered significant losses.

Table 3.2: Mean values of vegetation parameters in 2008 and 2019, with standard deviations in parentheses. mL, mF, mN: mean Ellenberg indicator values for light, soil moisture and nutrients. Differences in average values were examined with a Wilcoxon signed rank test. Arrows denote a significant increase or decrease over time, respectively.

	2008	2019	p
total richness	21.8 (4.9)	22.5 (6.2)	0.226
⇓ total cover	77.3 (10.6)	73.9 (16.7)	0.023
dry grassland character species			
number	6.9 (2.4)	7.3 (2.4)	0.054
⇑ % cover	40.1 (8.8)	49.2 (17.7)	<0.001
other poor grassland species			
⇓ number	4.2 (1.9)	3.6 (2.0)	0.003
⇓ % cover	16.4 (8.6)	12.4 (9.6)	<0.001
agricultural grassland species			
number	2.6 (1.7)	2.6 (2.0)	0.969
⇓ % cover	9.3 (7.9)	7.4 (6.7)	0.008
fallow indicators			
number	3.1 (1.8)	3.5 (2.3)	0.079
⇑ % cover	8.3 (6.1)	13.4 (13.7)	<0.001
ruderal species			
⇑ number	0.7 (0.7)	0.9 (0.9)	0.035
% cover	1.7 (1.9)	1.8 (2.2)	0.678
mL	7.24 (0.15)	7.26 (0.22)	0.103
⇓ mF	3.94 (0.24)	3.87 (0.30)	<0.001
mN	3.16 (0.42)	3.18 (0.48)	0.896
⇓ evenness	0.85 (0.06)	0.81 (0.11)	<0.001
⇓ grasses:forbs	1.19 (0.96)	1.16 (1.5)	0.031
⇑ *B. erectus* cover	12.6 (15.3)	16.6 (20.0)	0.008
⇓ *B. pinnatum* cover	9.6 (11.3)	5.5 (7.0)	0.001

3.3.3 Vegetation changes under different microclimatic conditions

The comparison of steep, south-facing slopes and flat/north-facing slopes reveals some important site differences in vegetation change between 2008 and 2019. Total species number, which was already lower on steep, south-facing slopes in 2008, decreased further on these sites, while it increased on flat or north-facing slopes (Figure 3.4). Turnover, expressed by the Sørensen index, was significantly lower on the driest sites. Differences in other indices between the two site types were not statistically significant, but contribute to the overall picture. Total cover generally decreased, but more so on steep, south-facing slopes. The number of dry grassland character species per plot tended to decrease on steep, south-exposed slopes, but to increase on sites with less extreme conditions. The same was true for the number of agricultural grassland species. The number of other grassland species with low nutrient demands generally decreased, while the number of ruderal species increased. Changes in mean Ellenberg indicator values were influenced by the microclimatic conditions in the sites, with steep, south-facing slopes showing higher mL and decreasing mN values. In contrast, flat or north-facing slopes increased in mN. Changes in the grasses-to-forbs ratio only differed slightly between the categories. Evenness decreased throughout, but more on south-facing sites.

In summary, the effects of the recent droughts were stronger on the driest slopes, resulting in a reduction of total species richness, including dry grassland character species. Signs of ongoing nutrient accumulation (increase in agricultural grassland species and mN) were present only in the moderately dry, north-facing sites.

The NMDS ordination of all sites in both years shows a summarising picture of the vegetation shifts between 2008 and 2019 (Figure 3.5). A general shift in the positive direction along the first axis is visible. This is associated with an increasing cover of ruderal species and a lower cover of poor grassland species not specially adapted to drought conditions. Total species richness and mF also decrease in this direction. The shift in species composition differed between flat/north-facing slopes and steep, south-facing ones. The latter moved slightly into the negative direction along the second axis. This is mainly correlated with an increase in cover of character species of dry grasslands and in mL, a reduction in total cover and fallow indicators. In contrast, communities on flat and north-facing slopes shifted slightly in the positive direction along the second axis, where mN and species of agricultural grasslands increased.

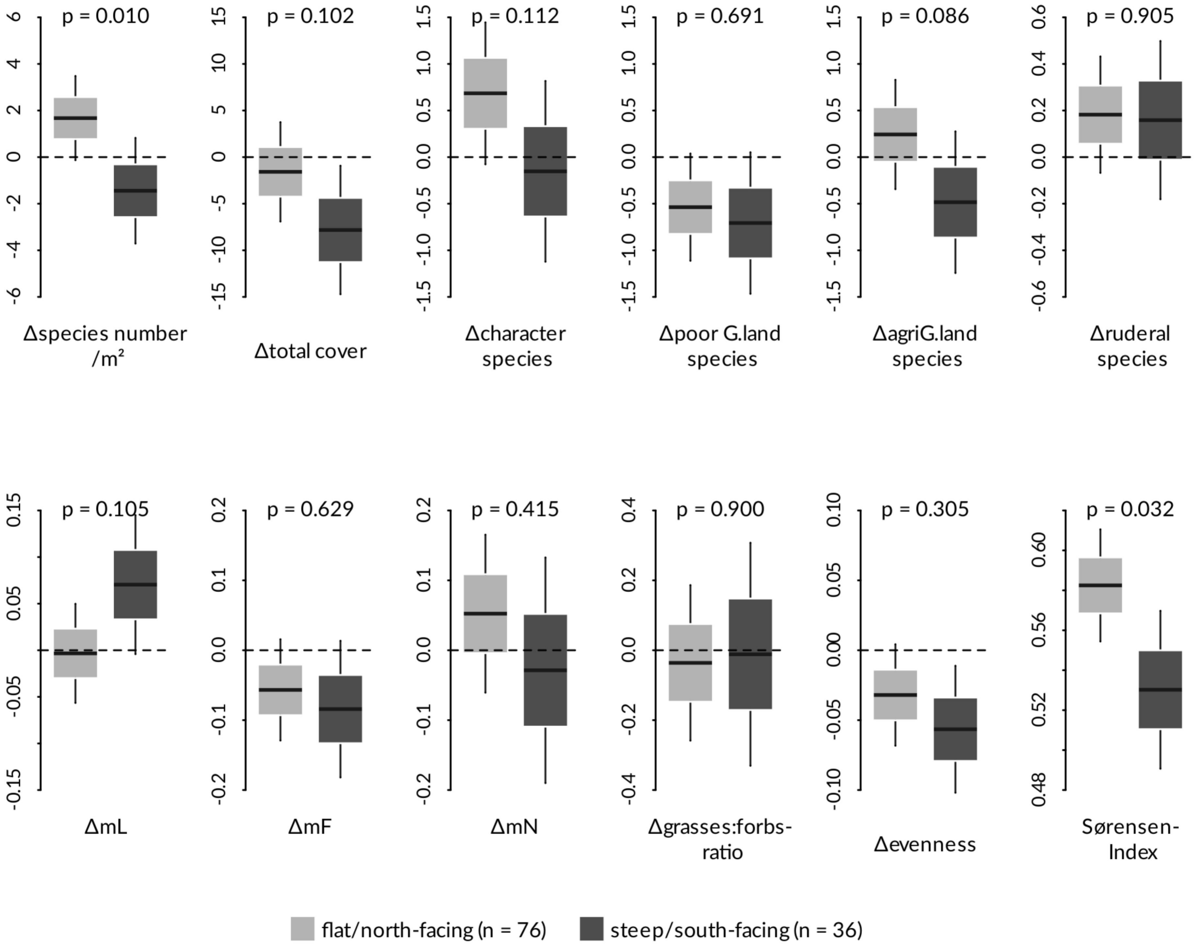

Figure 3.4: Results of linear mixed models showing the differences in vegetation change from 2008 to 2019 between the two categories steep/south-facing vs. flat/north-facing slopes. Shown are the predicted model values of the respective variable for both categories and their 95%-quantiles, with the effect fixed at the mean of the variable in 2008 and averaged over all 25 study sites. *p* values give the significance of difference between the two sites type categories. Δcharacter species, Δpoor G.land species, ΔagriG.land species, Δruderal species: differences in numbers of dry grassland character species, other species of nutrient-poor grasslands, species of agricultural grasslands and ruderal species per plot, respectively, between 2008 and 2019. ΔmL, ΔmF, ΔmN: differences of community weighted Ellenberg indicator values for light, soil moisture and nutrients between 2008 and 2019.

3.4 Discussion

3.4.1 H1: Particularly warm and dry microclimates generally have a positive effect on the characteristic species composition of dry grasslands.

In the initial survey in 2008, the typical species of calcareous grasslands were more abundant where topography created a particularly hot and dry microclimate, i.e. on steep, south-facing slopes, confirming our first hypothesis. In the models, a positive relationship between the heat index and the number of dry grassland specialists was found, as well as a negative

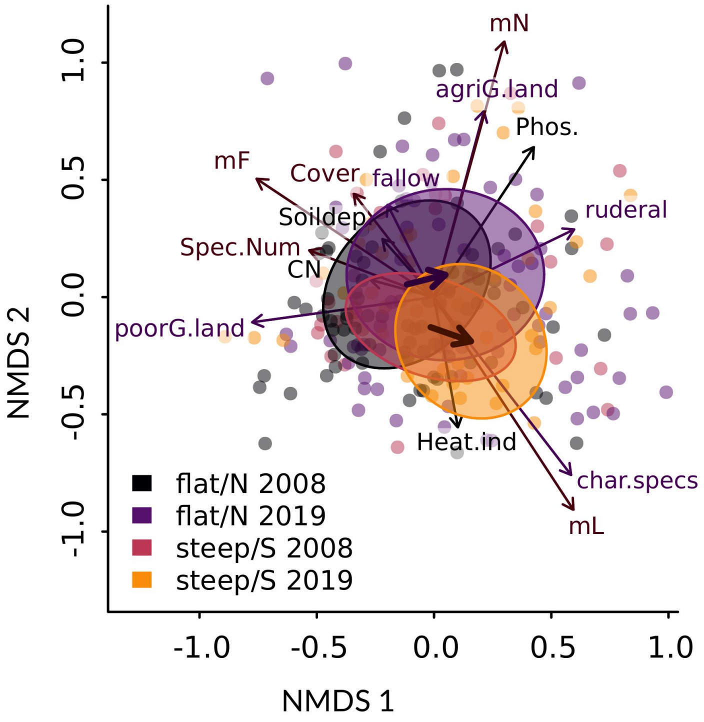

Figure 3.5: NMDS of square-root transformed vegetation data of both survey years. Ellipses mark the standard deviation of the points in the four groups. flat/N: flat and north-facing slopes in 2008 and 2019. steep/S: steep, south-facing slopes in 2008 and 2019. Arrows point from the centroid of the respective group in 2008 to the centroid of the same group in 2019. mL, mF, mN: Community weighted Ellenberg indicator values for light, soil moisture and nutrients. Spec.Num: Total species number per plot. char.specs: Share of cover of dry grasslands character species. poorG.land: Share of cover of species of other nutrient-poor grasslands. agriG.land: Share of cover of agricultural grassland species. fallow: Share of cover of fallow species. ruderal: Share of cover of ruderal species.

relationship between heat index and more mesic, nutrient-demanding and competitive agricultural grassland species. This is also reflected in a negative correlation between the heat index and mF and mN. The proportional cover and absolute number of dry grassland specialists were significantly higher on steep, south-facing slopes than on flat sites or north-facing slopes. This supports the idea that dry conditions can have a stabilising effect on the species composition in dry grasslands, as they push back more competitive species that are less well adapted to drought stress (Bennie et al. 2006; Fischer et al. 2020).

Soil nutrient conditions, especially phosphorus (P) availability, played an equally important role. These findings coincide with observations from Adriaens et al. (2006), who also identified productivity and insolation as the two main factors determining species composition in Belgian calcareous grasslands. We found a significantly positive relationship of P concentrations with indicators of eutrophication (share of agricultural grassland species, mF and mN). There was, however, no effect of P levels on evenness or the grasses-to-forbs ratio in the models. Calcareous grasslands are commonly considered to be P-limited (Carroll et al. 2003) and the atmospheric input of P is generally low. This explains why the influence of P was significantly greater than the influence of the C/N ratio in the models. Nutrient-demanding and competitive species are restricted to sites with sufficient P supply, while those with efficient P economies can avoid competition on less well-supplied sites.

In the context of eutrophication via atmospheric nitrogen deposition, the two factors of water availability and P supply can be interpreted as limiting factors in the sense of Liebig's law of the minimum (Liebig 1840). When water and/or phosphorus act as limiting resources, more productive species that are generally promoted by higher nutrient levels cannot fully exploit the deposited additional nitrogen. Therefore, the effects of eutrophication are weak on particularly dry and phosphorus-poor sites (Bennie et al. 2006; Dengler et al. 2014; Diekmann et al. 2014), which favours the specialised species of calcareous grasslands that are the target species for nature conservation in our sites.

Among the site-specific variables in the models, reflecting water availability, nutrient supply and management type, no significant predictors for total species richness were found. Yet, we did not account for variables characterising the surrounding landscape, such as management history, isolation, habitat area and diversity. Fragmentation and landscape context are known to be important factors for species richness in semi-natural grasslands (Adriaens et al. 2006; Zulka et al. 2014). Since site identity explained a big part of the variation in species richness (56 %), it is plausible that factors such as these strongly influenced total species richness. However, while total species number is often considered a measure of "quality" in ecology (Bobbink & Willems 1987), the number of specialised species is more important from the perspective of conservation.

3.4.2 H2: The species composition of semi-arid calcareous grasslands is generally robust to the exceptional droughts of the last decade

Contrary to results from experimental studies (Grime et al. 2008; Maalouf et al. 2012), the changes in vegetation between 2008 and 2019 show clear signs of the intense droughts of the last decade. Total cover and mF decreased significantly, an effect previously reported by e.g. Sternberg et al. (1999) and Morecroft et al. (2004). Species adapted to dry conditions, i.e. character species of dry grasslands, profited most over this period, as anticipated by Behrens et al. (2009) and Pompe et al. (2011). In contrast, grassland species adapted to low-nutrient conditions but not to drought declined most in number and cover. Agricultural grassland species, which are likewise not adapted to drought but are more nutrient-demanding, were not as severely affected and only decreased in cover, but not in species number. Ruderal species were able to benefit from the dry conditions, a process that was reported as "grassland ruderalisation after a drought event" by Fischer et al. (2020). The drought most likely acted as a disturbance and the resulting bare soil patches opened up opportunities for the short-lived and fast-colonising ruderal species. The spread of shrub and tree species points to a tendency towards less intensive land use of our study sites, even though they were all actively managed within conservation programs. These results represent conservative estimates of change, especially for fallow indicators, because overgrown areas in the sites were avoided while resampling to match the original methodology.

Evenness as a measure of diversity decreased over the course of the eleven years, indicating a more pronounced dominance structure. However, mean evenness in 2019 was still at a very high level (0.81), compared to other calcareous grassland sites (Haeupler 1982). As already pointed out by Bornkamm (2006), the dominance structure appears to be determined mainly by one species: *Bromus erectus*. In general, there was a significant spread of *B. erectus* whereas *Brachypodium pinnatum* simultaneously declined. The shift in the competitive relationship between these two grasses can be approached from several angles. *B. erectus* is a relatively late invader to the study area and was still very rare just 100 years ago (Bornkamm 2006). It may simply not yet have reached its final range. Secondly, *Bromus* is reportedly more drought tolerant than *Brachypodium* and has a higher colonisation ability after disturbance (Corcket et al. 2003). This might have given *Bromus* an advantage over *Brachypodium* during the drought spells. Thirdly, management as a complex factor composed of management type (mowing or grazing) and intensity (time of year, but also kind of animal, stocking density and grazing duration) may play an important, but difficult to disentangle role. It is known that *Bromus* is preferably eaten by grazers and *Brachypodium* is sensitive to early mowing or grazing (Leuschner & Ellenberg 2017b). The fact that all four sites where *Bromus* increased the most are under the management regime of one single municipality supports the theory that management had a strong influence on the species' dynamics.

3.4.3 H3: Changes in species composition and diversity induced by drought depend on the microclimatic conditions of the site

A different perspective emerges when differentiating between sites with varying levels of drought exposure. On steep, south-facing slopes, total species richness decreased, affecting all species groups except ruderal species. Remarkably, this also applied to character species of dry grasslands whose adaptations to dry conditions may be insufficient to endure the severity of the recent droughts on the sites with the most extreme microclimate. This is a first warning signal that some semi-arid grassland species may not be able to persist under the unfolding climate change scenarios that predict more intense and frequent droughts (IPCC 2014; DWD 2018). The increase in bare soil on steep slopes, together with the predicted increase in heavy rainfall events, may additionally lead to higher erosion. On the other hand, conditions on flat/north-facing sites promoted an increase in total species number and the share of specialised species, but also an increase in nutrient-demanding common species and higher mN values. These eutrophication processes, which are frequently observed in this type of grassland and pose a threat to species diversity (Bennie et al. 2006; Jandt et al. 2011; Bauer & Albrecht 2020), were apparently not halted even during a drought period. Consequently, if management and nutrient deposition continue as at present, the flat/north-facing sites cannot be seen as long-term refugia for mesic dry grassland character species, as the ongoing process of eutrophication by nitrogen deposition may hinder their establishment. The role of conservation strategies affecting biotic and abiotic framework conditions was highlighted by Petermann et al. (2007). The current impairment of calcareous grasslands through e.g. nutrient enrichment, area loss, fragmentation, and thus degradation of genetic diversity and loss of functional interrelations makes them more sensitive to additional stressors such as climate change (Petermann et al. 2007). For a conservation strategy adapted to climate change, it would be crucial to consider these aspects to ensure that sites with less extreme microclimates can serve as refugia in the future.

Species turnover was higher on the more mesic sites, a result also reported by Bennie et al. (2006). This is caused by greater changes in species cover values and more newly appearing species (gains) in north-facing plots, while the number of disappearing species (losses) did not differ between steep/south-facing and flat/north-facing sites. Lower turnover promises more stability and a better conservation of species and habitats. However, the direction of change is of great importance. In the present case, the more “stable” south-facing sites lost specialist species while these increased on the more “unstable” north-facing sites. Bennie et al. (2006) expressed the hope that more frequent and intense summer droughts might be profitable for the maintenance of stress-tolerant vegetation in the future. Our results confirmed the underlying assumption that higher drought intensities may inhibit eutrophication effects (see hypothesis 1). The authors did, however, not anticipate any negative effects that we now see after a decade in which increased summer drought events have become a reality.

Our results show that it can be important to differentiate even within a dataset of relatively homogeneous vegetation, not only between species groups with varying requirements, but also between sites with different microclimatic conditions. This allows us to identify more subtle changes or even opposing trends that may cancel each other out in the overall trend.

3.5 Conclusion

The characteristic vegetation of semi-arid grasslands is commonly thought to profit from global warming, either by an increase in potential habitat area or by the positive, competition-reducing effects of droughts on the specialised species of these habitats. However, a substantial expansion of habitat area is unlikely in Europe’s intensely used landscape, as the vegetation relies on traditional land use practises mostly only applied for nature conservation reasons. Our results confirmed that a warmer and drier microclimate promoted the specialised vegetation in the past, but this may no longer be the case with ongoing climate change. Steep, south-facing sites lost species from all groups except ruderal species after a decade of intense drought, while species numbers increased on flat or north-facing sites. On these, eutrophication processes seemed to continue despite the intense drought period.

3.6 List of Appendices

Figure A4: Map of the 25 study sites in North-West Germany.
Table A9: Summary of mixed linear models for vegetation variables in 2008.

3.7 Acknowledgements

We thank the local authorities of south Lower Saxony for permission to work in the various natures reserves. Andreas Suchopar and Marion Albrecht did the soil chemical analyses and Martina Tsaliki helped with the field work.

3.8 Data availability statement

The data underlying this study and the R scripts used are available at Figshare (10.6084/m9.figshare.17000650.v2).

3.9 References

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— Chapter 4 —

Regression to the mean in vegetation science

Leonie Mazalla & Martin Diekmann (2022)
Journal of Vegetation Science, 33: e13117
https://doi.org/10.1111/jvs.13117

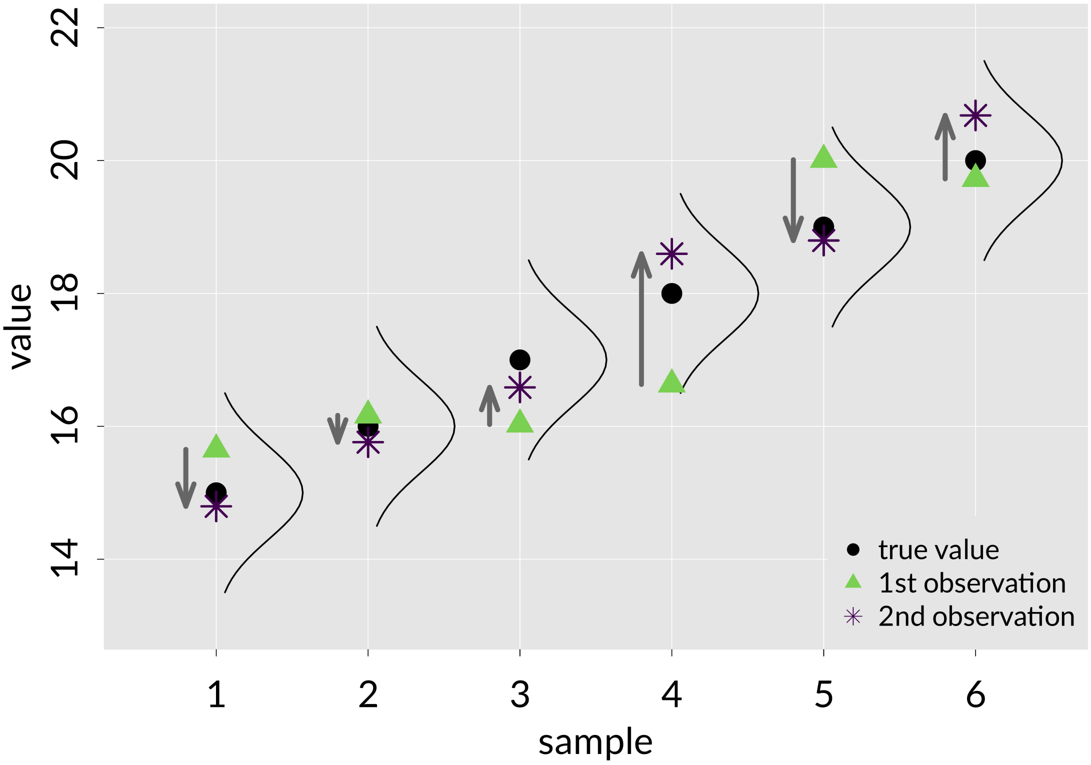

Illustration of the regression to the mean effect. True values of observed variables are unknown and their measurement inevitably includes an error term, here illustrated by the normal distributions. Values that were accidentally overestimated in a first observation and likely to be reduced in a second observation.

Abstract

Aims
We present a possible pitfall in the statistical evaluation of vegetation resurvey studies and longitudinal experimental studies caused by the stochastic phenomenon called "regression to the mean". It manifests itself in a negative correlation of change scores (the difference between an initial and a follow-up measurement) with the initially measured values. If disregarded, analyses of the drivers of change may be misleading. The aim of this paper was to raise awareness of this issue in vegetation science.

Methods
The relevance of "regression to the mean" is shown using four exemplary datasets, two from grasslands and two from forests with time gaps for the survey periods between 11 and 32 years, using in total 26 variables. The stochastic mechanism behind it is explained in detail and visualised with artificial data. A suggestion for how to deal with this phenomenon in the analysis of models regressing change in a variable on a predictor variable is made based on one of the exemplary datasets.

Results
We found the effect of "regression to the mean" in 24 out of 26 examined variables. It also had a significant impact on the results of models that aimed to explain the change in an observed variable (e.g. change in species number) with another variable (e.g. soil nitrogen content).

Conclusions
The effects of "regression to the mean" are important to keep in mind when interpreting results of resurvey studies, but also when evaluating treatments in experimental studies. We propose to always include the initial values of a variable as a predictor when calculating models of its change scores or evaluating treatment effects. This is especially important when the initial values are already correlated with potential predictor variables.

Keywords biostatistics, modelling, regression to the mean, resurvey studies, statistical methods, stochasticity, treatment effect, vegetation change

4.1 Introduction

Regression to the mean (RTM) is a statistical phenomenon that occurs when repeated measurements are made on the same subject of observation. It is based on the fact that stochasticity always plays a role when measuring data, be it through measuring error or the dynamics of nature itself. Therefore, in a first measurement there will be some data points that deviate from their "typical" value, or the long-term average. If we assume a normal distribution for these deviations, such data points will probably be closer to their long-term average in a follow-up measurement. They will appear to have "regressed to the mean". Of course, this does not need to be the case for every single data point, but over an entire dataset the effect adds up to a phenomenon that can be observed regularly (Barnett et al. 2005; Aickin 2009). It manifests itself in a negative correlation of change scores (the difference between an initial and a follow-up measurement) with the initially measured dataset. This means that the changes in, for example, species number over time are often negatively correlated with species number at the initial measurement. This correlation is an artefact of stochasticity in the data and should be interpreted with much care (Barnett et al. 2005).

RTM also occurs in everyday situations. One example: Students who had the highest scores in a first test tend to get lower scores in a second test (although there will likely be a positive correlation between the results of the first and the second test across all students). Of course, their results mainly depend on skill, but luck (= stochasticity) may have played a role as well. It is unlikely that the luckiest students in a first test will be as lucky in a second test. In vegetation science, stochastic fluctuations of measured values over time are to be expected regularly, on the one hand because vegetation is dynamic, on the other hand due to measurement uncertainties, e.g. through location or observer bias in resurvey studies (Palmer 1993; Verheyen et al. 2018).

The phenomenon of RTM can have important implications for the statistic evaluation of change scores (Barnett et al. 2005; Aickin 2009). However, we have found little evidence of awareness about this statistical artefact in the field of ecology. Studies from the field of vegetation science that perform analyses with change scores do not mention RTM (e.g. Verheyen et al. 2012; Britton et al. 2017; Mitchell et al. 2018; Hester et al. 2019; Peppler-Lisbach et al. 2020; Ridding et al. 2020). A search in the Web of Science for the keywords "veget*" and "regression to the mean" revealed only two publications. The only manuscript with "regression to the mean" in the title (Wamelink et al. 2004) appears to refer to another concept, namely "regression dilution" (see Frost & Thompson 2000). A second paper by Wamelink et al. (2011) also mentions RTM in the methods section. Here, however, the authors refer to the phenomenon of axis shrinkage as a result of averaging, which is another concept that might be confused with RTM. This short literature search shows that RTM is not well known in vegetation science and can easily be confounded with other phenomena. One notable exception is the publication by Palmer (1993), which nicely illustrates issues with RTM in vegetation sampling and monitoring. However, the author and the publications citing him focus on the design of monitoring or resurvey studies, i.e. site or species selection, and do not address the implications for statistical analyses.

In other fields, especially medicine and psychology, the issue of RTM is widely discussed, namely in the statistical evaluation of treatment effects. A similar search as mentioned above, but with the keyword "medic*", revealed more than 250 papers from the medical sciences with the phrase "regression to the mean". Consequences of neglecting RTM were, for example, shown by Hannon et al. (2019). They criticise a study in which the use of a drug supposedly led to a greater weight loss in patients that were more overweight at the start of the study. The original authors did not take into account that the first weight measurement inevitably involved some stochasticity and that the patients with the highest initial weights therefore already lost weight through RTM alone. The effect of the drug was therefore overestimated. More examples from the field of medicine are given in the reference section of Hannon et al. (2019). This issue of subgroup selection is also treated by Palmer (1993). If one were to subjectively select for sampling the plots promising the highest number of species (i.e. the group of patients with the highest weights), it is quite likely that these values would be lower in a subsequent sampling, simply because they tend to be closer to their long-term average (Palmer 1993; Barnett et al. 2005).

To estimate the effect of a treatment in a proper way, correcting for RTM by taking the initial measurements into account is the standard procedure in the medicinal sciences (Barnett et al. 2005; Aickin 2009; EMA 2015). In this method paper, the concept of RTM is discussed with respect to vegetation resurvey studies that have received increased attention over the past years, as they offer empirical, plot-based data on vegetation changes and their underlying factors (Hédl et al. 2017). Exemplary datasets are used to show the relevance of the issue and artificial data to visualise the basic principles behind it. Finally, some recommendations for the statistical evaluation of variable changes in resurvey or experimental studies are made.

4.2 Does regression to the mean regularly occur in resurvey studies? Four exemplary datasets

We tested 26 variables with repeated measurements from four datasets for a correlation of change scores and initial values. Very strong evidence ($p < 0.001$) of a negative correlation was found in 18 of them and moderate to strong evidence ($0.001 < p < 0.05$) for another 6. The variables were: mean Ellenberg indicator values (12) (Ellenberg et al. 1992), species number (4), tree/herb layer cover (6), and soil pH (4). The four datasets originate from resurveys from two grassland types (calcareous grasslands, Diekmann et al. 2014, and acidic *Nardus* grasslands, Mazalla et al. 2021) and two forest types (ancient oak-hornbeam forest, Strubelt et al. 2019, and birch-oak forest, Strubelt 2019) which were recorded over time spans from 11 to 32 years (for details, see Table A12). Figure 4.1 shows the results for the variable

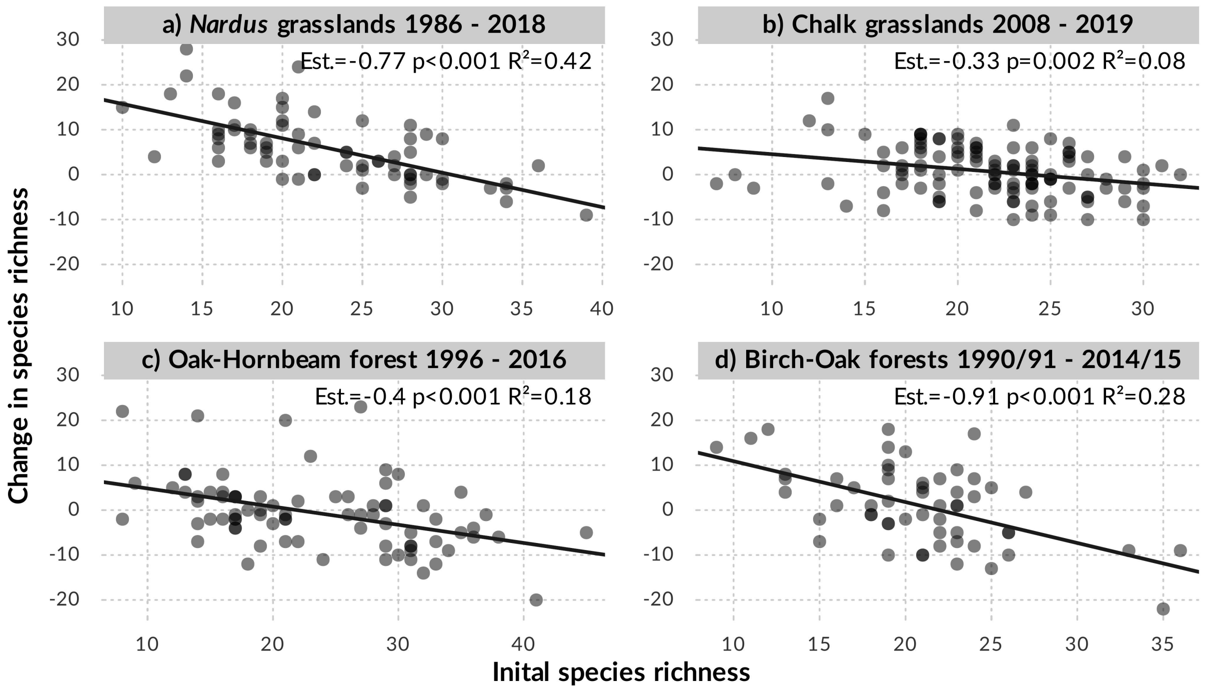

Figure 4.1: Difference in species number per plot between two survey periods plotted against initial species numbers at the first survey for four different resurvey datasets. a) *Nardus* grasslands surveyed in 1986 and 2018, Eifel mountains, Germany, b) chalk grasslands surveyed in 2008 and 2019, southern Lower Saxony, Germany, c) ancient oak-hornbeam forest surveyed in 1996 and 2016 near Bremen, Germany, d) birch-oak forests surveyed in 1990/91 and 2014/15 in Lower Saxony, Germany. Simple linear models are applied and the resulting coefficients given as annotation.

"species number". They are at least partly an effect of RTM: Sites with particularly low species numbers in the initial survey tended to have higher species numbers in the follow-up survey. Conversely, sites with very high species numbers in the initial survey tended to have fewer species in the resurvey. This was most likely independent of actual change going on at the sites. Other variables than species number, for example environmental measurements like soil pH or mean Ellenberg indicator values, also regularly showed negative correlations between initial values and change scores (Figure 4.2).

4.3 Simulating data to illustrate the mechanism behind RTM

4.3.1 Resurvey study setup

To visualise the stochastic mechanism behind RTM (as similarly explained in Barnett et al. 2005), we created a simple artificial dataset for "species counts". We made up "first year measurements" (*initial*) by drawing a random value for 100 "sites" from a normal distribution with mean = 15 and standard deviation = 1. This means that each site had a "typical" species number (= 15, "typical" in the sense of long-term average) and that the

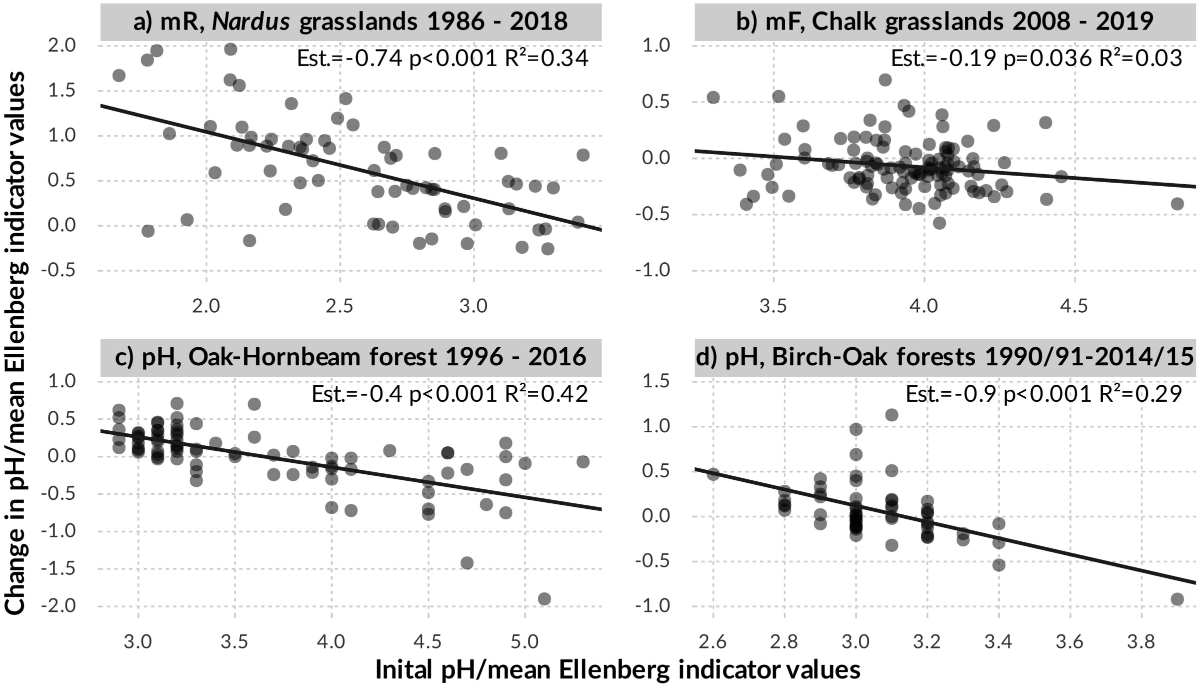

Figure 4.2: Differences in soil pH and mean Ellenberg indicator values per plot between two survey periods plotted against initial values at the first survey for four resurvey studies. mR = mean Ellenberg indicator value for soil reaction, mF = mean Ellenberg indicator value for soil moisture. a) mR in *Nardus* grasslands surveyed in 1986 and 2018, Eifel mountains, Germany, b) mF in chalk grasslands surveyed in 2008 and 2019, southern Lower Saxony, Germany, c) soil pH in an ancient oak-hornbeam forest surveyed in 1996 and 2016 near Bremen, Germany, d) soil pH in birch-oak forests surveyed in 1990/91 and 2014/15 in Lower Saxony, Germany. Simple linear models are applied and the resulting coefficients given as annotation.

observed value fluctuated around the mean with a standard deviation of 1. Values were rounded to integers. For better comprehensibility, we present the command used in R (R Core Team 2020) for this purpose.

$$initial = round(rnorm(100, 15, 1))$$

We then created “second year measurements” ($resurvey$) under the assumption that no directional change had happened. They were drawn independently from the same distribution and with the same command as for $initial$.

Figure 4.3a shows the frequency distribution of the values. There was no correlation between the measurements from year $initial$ and year $resurvey$, because they were independently and randomly drawn. Figure 4.3b visualises the measured values in $initial$ and $resurvey$ under the distribution from which they were drawn. Arrows point from one site’s value at time point $initial$ to its corresponding value at time point $resurvey$. Arrows from the lowest and highest values in $initial$ are highlighted in yellow. It shows that sites with initial values from the upper end of the normal distribution tended to have lower values at the second measurement and therefore negative change scores, and vice versa. When plot-

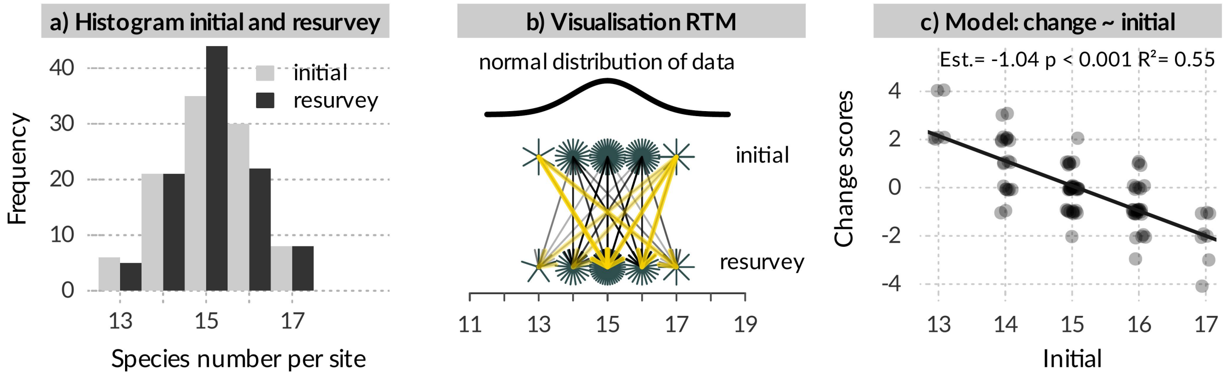

Figure 4.3: Visualisation of RTM in an artificial dataset. a) Histogram of "species numbers" drawn from a normal distribution with mean = 15 and standard deviation = 1 for two "time points" *initial* and *resurvey*, b) Distribution of values at time points *initial* and *resurvey*. Arrows indicate values of the same "site" at the respective time points. Each line in the circles represents one data point. c) Change scores ($resurvey - initial$) plotted against initial values. Positions of points are slightly shifted to show overlapping data points.

ting the difference between the two measurements ($resurvey - initial$) against the initial value, a negative correlation becomes apparent (Figure 4.3c). There is very strong evidence for a negative correlation of the difference between pairwise values randomly drawn from the same distribution for two different "time points" with the values of the first "time point"! The total variance of the dataset is not reduced, as data points initially lying in the middle of the distribution may now show greater deviations from the mean.

This relationship modelled here has no ecological meaning. There were no underlying patterns designed into the data, just two independent draws from the same normal distribution. RTM occurs, in the sense that sites with high values in the first measurement tend to have lower values at the second measurement and sites with lower values in the first measurement tend to have higher values at the second time point, just because this is more likely when drawing values independently from a normal distribution.

4.3.2 Experimental setup

As initial measurements, we created artificial species numbers for 100 plots, drawn as above from a normal distribution, this time with mean = 25 and standard deviation = 5. The first 50 plots served as "control" plots and were sampled a second time in the same way (*control*). The second 50 plots received a "treatment" that caused the "typical" species number to decrease by 3 (*treated*). Therefore their values were now drawn from a normal distribution with a mean of 22 and a standard deviation of 5. A categorical "treatment" variable was created that equalled "0" for the *control* plots and "1" for the *treated* plots.

To test the effect of the treatment, a simple method would be to compare the change in the *treated* group with the change in the *control* group, using either a linear model that relates the change scores to the *treatment* variable or a t-test of the change scores. In our simulated dataset, these methods revealed no evidence of a difference between the two groups, with an estimate of -1.78 for the difference in mean change between the *control* and *treated* group (Figure 4.44, Table 4.1a).

If, however, the initial species number was added to the model, strong evidence of an effect of the treatment variable emerges with an estimate of -3.22 (Table 4.1b). Figure 4.4b illustrates the difference between the two approaches. With the model in Table 4.1a, we compared the difference between the two dashed lines, the mean change scores. With the model in Table 4.1b, the difference between the solid lines is examined. Here, each plot's change score is adjusted according to their initial measurement prior to fitting the treatment effect (Barnett et al. 2005).

The two results differ in significance because the *control* group, by chance, had slightly higher values at the initial measurement (mean 25.7) than the *treatment* group (mean 24.2). We can therefore expect RTM to cause a slight decrease in the *control* group, which weakens the effect of the treatment when comparing change scores without correcting for RTM. In the opposite case, if initial *control* group values would have been lower, they would have tended to show an increase due to RTM. Thereby, a simple comparison of change scores would have overestimated the effect of the treatment.

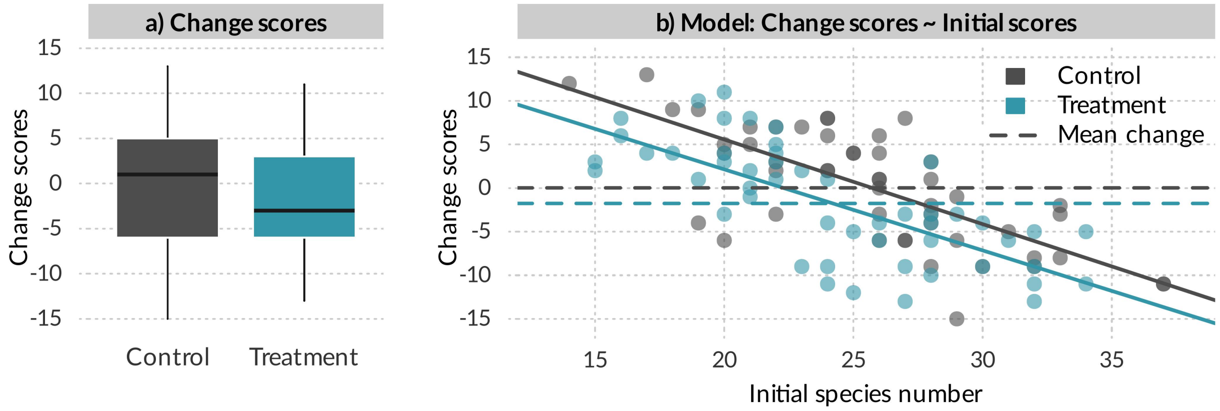

Figure 4.4: Visualisation of RTM in a simulated experiment. a) Change scores of species number in the two groups *control* and *treated*. b) Change scores of species number in the two groups *control* and *treated* plotted against initial species number. Dashed lines show the mean in change scores per group. Solid lines show a linear model fit of change scores against initial scores for the two groups.

4.4 Why should regression to the mean be considered in resurvey studies?

First of all, the effect of RTM (i.e. the negative correlation of change scores with initial values) should not without further thought be interpreted as a genuine ecological process. In all the exemplary datasets of the second section, we can observe that the most species-rich plots in the initial survey tended to lose species. This might be taken as an alarming sign of biodiversity loss, but probably has no ecological background. The same line of

Table 4.1: Model coefficients of the linear models relating species number change per plot to a) only the categorical variable "treatment (1/0)" and b) the categorical variable "treatment (1/0)" plus initial species number as a second predictor variable.

	a) Change scores ∼ Treatment			b) Change scores ∼ Initial + Treatment		
	Estimate	*p*	Adjusted R^2	Estimate	*p*	Adjusted R^2
Intercept	0.02	0.980	0.01	24.43	<0.001	0.52
Initial species number	–	–		−0.95	<0.001	
Treatment (yes)	−1.78	0.181		−3.22	0.001	

argument is explained in more detail in Palmer (1993). This does not necessarily imply that relationships like these never reflect an ecological process. For example, the greater increase in pH (and also mR) from initially lower values in the datasets in Figure 4.2 may be related to a recovery from acid rain since the 1980s. Base-rich rock weathers exponentially faster at lower pH values (Scheffer & Schachtschabel 2010), therefore pH and possibly also mR recover more strongly from initially lower pH values.

4.4.1 Why is this a problem especially with models of vegetation change?

Models of change are models that seek to explain the change in a variable (e.g. in species number) through a set of predictors (such as pH or management). Often, the initial measurement of the variable whose change we wish to explain is already correlated with the predictor variable. Here, we demonstrate the resulting effects with an example. The influence of soil nitrogen content on the change in species number in an oak-hornbeam forest near Bremen, Germany, between 1996 and 2016 is analysed. In the first survey year, there was very strong evidence of a negative relation of species number per plot with soil nitrogen content (Figure 4.5a).

As shown with all exemplary datasets in Section 4.3.2 (Figure 4.1c), there was a negative correlation between the change in species number and the initial species number in this dataset. From the combination of these two observations we can conclude that:

1. Sites with higher nitrogen levels had lower species numbers in 1996 → following RTM, they are expected to rather gain species.
2. Sites with low nitrogen content had higher species numbers in 1996 → these are in turn expected to rather lose species.

This is in fact the case when looking at the raw data (Figure 4.5b). The soil nitrogen content is positively related to species number change, although this relationship is weak (Table 4.2a). However, when we add to this model the initial species number in 1996 as a

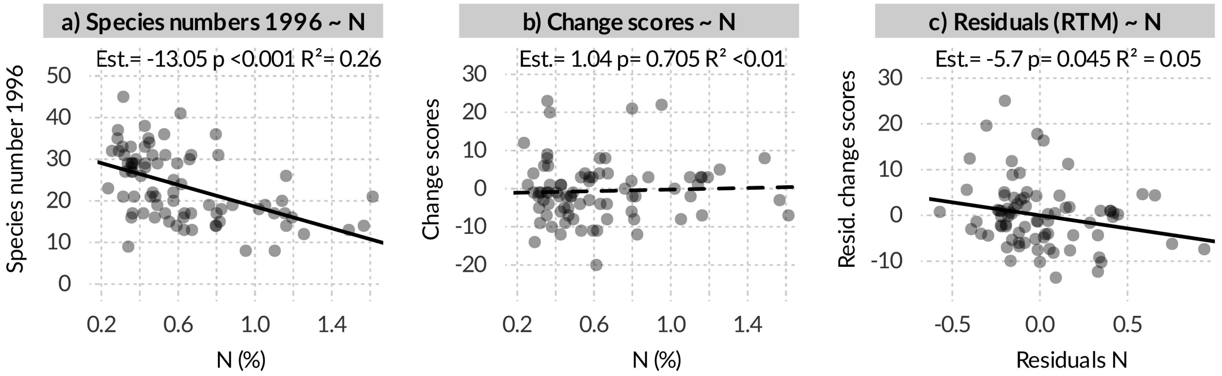

Figure 4.5: Relationship of species number and species number change between 1996 and 2016 with soil nitrogen content in ancient oak-hornbeam forest plots near Bremen, Germany. a) Species number per plot in 1996 plotted against the site's soil nitrogen content. b) Difference in species numbers per plot between 1996 and 2016, plotted against the site's soil nitrogen content. c) Residuals of the linear model "differences in species number $\sim$ initial species number" plotted against the residuals of the linear model "nitrogen $\sim$ initial species number". Simple linear models are applied and the resulting coefficients given as annotation. The dashed line indicates a non-significant fit.

second predictor variable, the influence of nitrogen content on species number change becomes negative instead of positive with moderate evidence that this is a relevant relationship ($p = 0.045$, Figure 4.5c, Table 4.2b). When interpreting this result, the overall R^2 should be separated into its components to not overestimate the predictive power of the nitrogen variable. This model gives a more appropriate impression of the relationship between nitrogen levels and the change in species numbers, as both were thus made independent of the original species numbers. This procedure is not limited to simple linear models, but is only presented in this way here for the sake of clarity.

Table 4.2: Model coefficients of the linear model regressing a) the change in species number per plot between 1996 and 2016 with soil nitrogen content and b) species number change per plot between 1996 and 2016 with soil nitrogen content and the initial species number in 1996 as a second predictor variable.

	a) Change scores $\sim$ Nitrogen			b) Change scores $\sim$ Initial + Nitrogen		
	Estimate	p	Adjusted R^2	Estimate	p	Adjusted R^2
Intercept	-1.27	0.513	total: -0.01	15.09	<0.001	total: 0.21
Initial species number	–	–	–	-0.52	<0.001	partial: 19.0
Soil nitrogen (%)	1.04	0.705	partial: -0.01	-5.70	0.047	partial: 0.02

Which model provides the more correct, ecologically relevant, result? Looking at the raw data, sites with high nitrogen contents did gain more species (Figure 4.5b). However, the positive influence of nitrogen on species number change was not stronger than the stochastic effect of RTM. Therefore, the statement that nitrogen did have a negative effect on the change in species numbers (Table 4.2b) is probably more valid. Nonetheless, there is room for interpretation. A hypothetical process of nutrient reduction could have led to an increase in species numbers on the more nitrogen-rich and therefore species-poor plots. In this case, however, this effect would have remained visible after correction for RTM. This is indeed true for the variable “tree layer cover” in the same study, which was reported to have a negative effect on the change in species number (Strubelt et al. 2019, Table 5). This result did not change after correction for RTM (see Table A10, A11).

4.5 Summary and recommendations

In this manuscript, we have addressed the phenomenon of RTM from a theoretical and practical viewpoint. We believe that there should be more awareness of this phenomenon in vegetation science. It is important to keep in mind when analysing results of resurvey studies, but also when evaluating treatments in experimental studies. To minimise the risk of RTM distorting study results, Palmer (1993) advised to carefully design studies in a way that the initial sampling does not produce a built-in bias. For example, when monitoring rare species, he recommends to not only place plots where the species is initially abundant, but also where it is rare or even absent. When calculating models of change scores or evaluating treatment effects, we propose to always include the initial values of the variable as an additional predictor (Barnett et al. 2005; Aickin 2009; EMA 2015). This is especially important when the initial values were already correlated with potential predictor variables. If disregarded, predictor variables may appear significant even though they are not (or vice versa) simply because they correlate with a stochastic effect. If the effect of RTM is minor for the variable at hand, there should generally be no disadvantage of including the initial measurements in a model, since this will not change the overall outcome (Table A10, A11). As often with models, in this case it will be the choice of the author to decide for the ecologically most meaningful model.

To gain further insight into the typical prevalence and magnitude of the effect of RTM (e.g. R^2 values, slope of estimates) in vegetation science, we would need a larger number of datasets from resurvey studies or experiments. This would enable us to better separate the contribution of RTM to the relationship between change scores and environmental variables from actual ecological processes.

4.6 List of Appendices

Table A12: Sources of the four exemplary datasets from resurvey studies.
Table A10: Model coefficients of the linear model regressing the change in species number plot between 2002 and 2020 with soil potassium (K) content.
Table A11: Model coefficients of the linear model regressing the change in species number

per plot between 2002 and 2020 with soil potassium (K) content and species number in 2002 as a second predictor variable.

4.7 Acknowledgements

We thank Cecilia Dupré, Gerhard Ludwig, Ilka Strubelt, Martina Peters, and Thilo Heinken for contributing to the datasets used in this publication.

Data availability statement

The data underlying this study and the R scripts used are available at Figshare (doi: 10.6084/m9.figshare.16559988).

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— Chapter 5 —

Baseline turnover: accounting for stochasticity in studies of vegetation change

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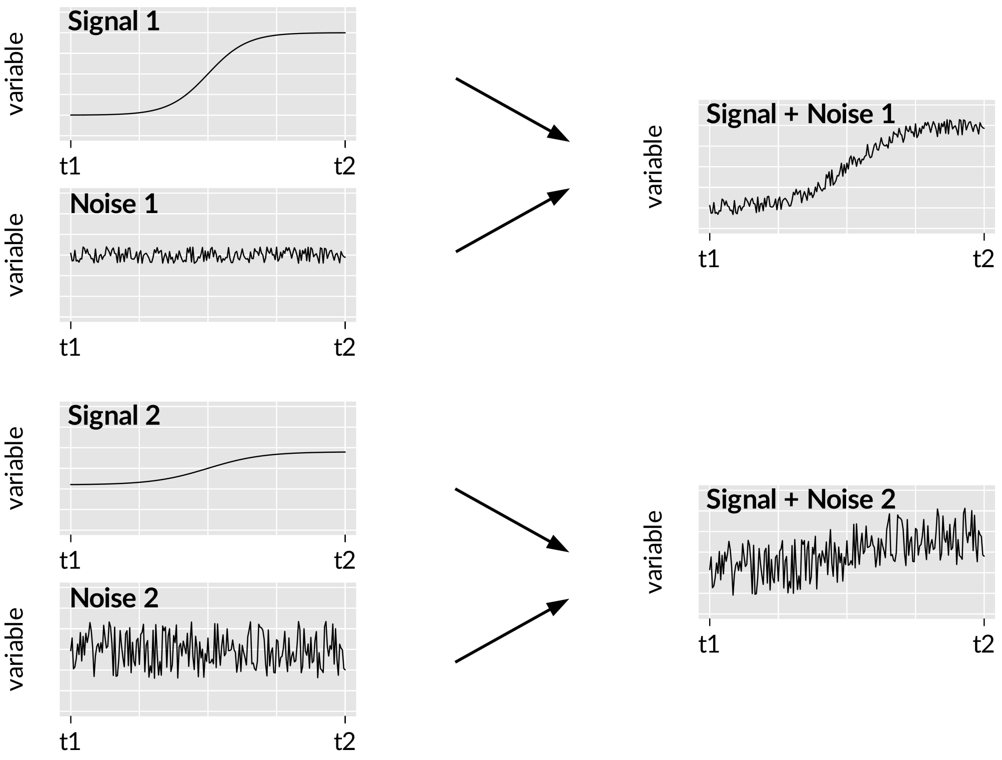
Journal of Vegetation Science, submitted.



High levels of noise or stochasticity in the data may obstruct the signal that is meant to be observed. This is especially important if the signal itself is weak.

Abstract

Aim

Quantifying vegetation dynamics is of paramount importance in a time of rapidly changing environments and human impact on nature. Observed vegetation change can be divided into three components: directional change (e.g. loss of cold-adapted species due to warming); methodological pseudo-turnover (e.g. as a result of relocation error); and stochastic fluctuations, which are here referred to as “baseline turnover”. In this paper, we provide estimates of the magnitude of baseline turnover in nine vegetation types worldwide and aim to identify its relevant drivers.

Methods

We analysed 57 time series datasets of permanent plots gathered in nine vegetation types (ranging from desert to forests) with time series ranging from 5 to 87 consecutive years. Dissimilarity per plot over time was calculated using eight different dissimilarity indices (Sørensen, Jaccard, Simpson/Lennon, Hellinger) employing both presence/absence- and cover-based versions which were then fitted to their temporal distance. The y-intercept, i.e. the theoretical dissimilarity at zero temporal distance, was used as an estimate of baseline turnover. Finally, the influence of multiple biotic and abiotic drivers on baseline turnover was analysed using mixed-effects models.

Results

Estimates of baseline turnover differed markedly between vegetation types, ranging from 0.04 to 0.41 for the Sørensen dissimilarity index (presence/absence-based). Desert vegetation had the highest baseline turnover, followed by steppe/prairie vegetation. Semi-natural temperate grasslands and forest understory, together with alpine vegetation, followed in descending order. Larger vegetation plots and higher saturation from the regional species pool resulted in lower baseline turnover, whereas this increased with mean annual temperature and annual species proportion.

Conclusions

Our study helps to disentangle the role of stochastic processes in community assembly and local biodiversity change over time. Determining baseline turnover values may help researchers to assess whether dissimilarities between resurveyed plots are the result of random fluctuation or can be attributed to directional vegetation change.

Keywords: dissimilarity index, Hellinger, Jaccard, neutral theory, pseudo-turnover, resurvey, Simpson, Sørensen, stochasticity, vegetation dynamics

5.1 Introduction

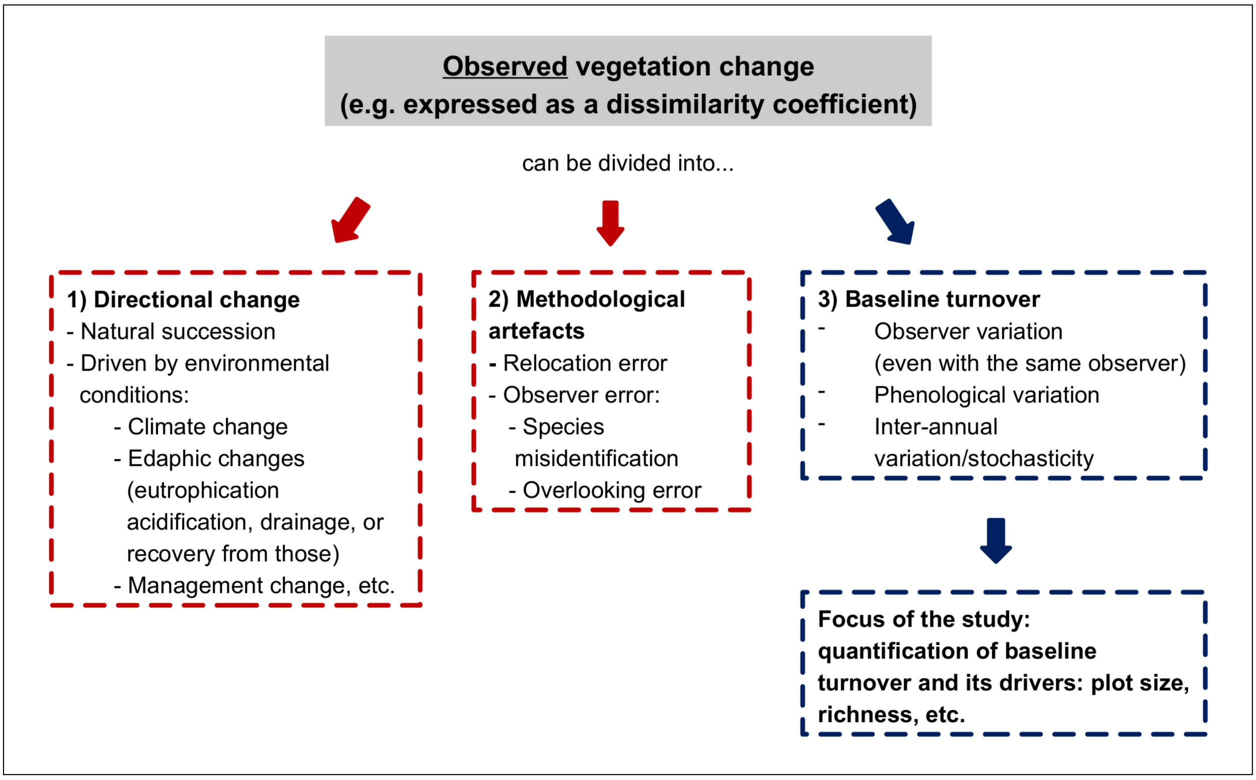
The observation and interpretation of temporal vegetation change has a long history in the field of vegetation science. Quantifying temporal dynamics has become increasingly important on account of a rapidly changing environment and human impact on nature, which is reflected by the growing number of available permanent plots (Bello et al. 2020; Knollová et al. 2024) and resurvey studies (Kapfer et al. 2017). Dissimilarity indices are commonly used to asses observed vegetation change, measuring the degree of compositional differences between two plots that are spatially or temporally distant (e.g. Rolim et al. 2017; Diekmann et al. 2019). High dissimilarity values are often recognised as a sign of a shift in vegetation composition, potentially altering ecosystem services or stability (Collins et al. 2000). One of the biggest challenges in the study of vegetation change is to disentangle the observed change into ecologically interpretable change (hereafter "directional change") from pseudo-turnover caused by methodological artefacts (Collins et al. 2000; Kapfer et al. 2017; Verheyen et al. 2018). In particular, two common sources for methodological artefacts have been identified: observer error and relocation error (Morrison 2016; Verheyen et al. 2018). Observer error includes apparent differences in species composition due to human error, i.e. species misidentification or the overlooking of species. This type of error can occur not only between two observers, but also when the same person surveys the plot under different conditions (Morrison 2016). On the other hand, relocation error arises when the original position of a plot is unknown, so the location of a follow-up survey differs from the original survey. On average, a 10 % to 30 % dissimilarity in species composition has been found as a result of methodological pseudo-turnover (Morrison 2016; Verheyen et al. 2018; Boch et al. 2022). Nevertheless, the extent to which stochasticity contributes to observed vegetation change is rarely considered in resurvey studies.

To address this challenge, we focused on stochastic temporal fluctuations in species composition over time. We developed a conceptual framework in which differences in vegetation between two points in time, quantified by a dissimilarity index, are divided into three components (Box 1): 1) Directional change, including succession or change driven by environmental factors – e.g. climate change or land use change; 2) Pseudo-turnover, caused by methodological artefacts like relocation or misidentification error (hereafter "methodological pseudo-turnover"); and 3) "Baseline turnover" – the focus of this paper – which is the stochastic component of species turnover in the absence of directional trends. This latter component excludes short-term fluctuations that seem random at first on account of incomplete knowledge of potential drivers but could, nevertheless, result from external factors, such as weather conditions (Vellend et al. 2014; Fischer et al. 2020). While, in theory, methodological pseudo-turnover can be excluded by applying appropriate methodology (e.g. permanent plots, experienced observers), we acknowledge that baseline turnover may contain some amount of pseudo-turnover due to inevitable methodological uncertainties. Although the use of appropriate precautions can reduce observer error, human observers will always generate inaccuracies in their recordings (Morrison 2016). Similarly, phenology will never be identical for two observation periods even when the selected resurvey season is the same as the original (Vymazalová et al. 2012).

The estimation of the stochastic component in vegetation composition has a long theoretical background. The carousel model (van der Maarel & Sykes 1993), for instance, proposes that it is actually a matter of chance which species occupies a particular microsite over time in rather small-scale, homogeneous environments. On a much larger scale, the unified neutral theory (Hubbell 2001) goes further, suggesting that all species are demographically equal in fitness, and that their co-occurrence over time is only limited by dispersal. Although these concepts are highly debated, some degree of stochasticity in the occurrence of species in a plot from year to year is likely to occur (Collins et al. 2000; Bakker et al. 2023).

With regard to the estimation of the magnitude of stochasticity, this has been, up to now, based exclusively on spatial autocorrelation. In particular, Brownstein et al. (2012) identified, for different vegetation types in New Zealand, the theoretical amount of dissimilarity at a modelled spatial distance of zero by calculating the "nugget" (i.e. the intercept) of a model which relates plot dissimilarities to their spatial distances. Following Brownstein et al. (2012), differences in conditions between plots (e.g. weather conditions or propagule rain) should decrease as their distance from each other decreases. At a theoretical distance of zero, the only remaining component which can explain differences in species composition is chance. In the current study, we present the first benchmarks for quantifying the amount of stochasticity in vegetation composition for different vegetation types worldwide using time series data. The magnitude of baseline turnover was quantified following the method employed by Brownstein et al. (2012) by estimating dissimilarity values of the vegetation composition of the same plot at zero temporal distance.

A large dataset of vegetation samples was compiled using data from 15 countries worldwide, mainly located in the temperate zone (Figure 5.2, 5.3). Permanent plots were sampled from 5 to 87 consecutive years, ranging in size from 0.01 m^2 to 400 m^2. Vegetation types included deciduous and evergreen forest understory, steppe/prairie vegetation, semi-natural grasslands, dune vegetation, (succulent) desert vegetation, alpine vegetation and a single mire. In order to ensure comparability with a wide range of studies, benchmarks were calculated based on the four most commonly used dissimilarity indices and their abundance-based versions (Sørensen, Jaccard, Simpson, and Hellinger; see Table A13 for definitions). In this way, we aimed to make a contribution towards disentangling the observed vegetation change into artefacts and directional change. We also attempted to identify the main drivers of baseline turnover, hypothesising that an important role is played by the life span of present species, plot size, species richness and climatic variables. We expected annual species location to be more irregular than that of perennials, since annuals appear or disappear more frequently from a delimited space, such as a vegetation plot, thus resulting in higher levels of stochasticity in the observations. We also expected baseline turnover to be lower in bigger plots, analogous to relocation error (Kopecký & Macek 2015). Species composition over time is probably more stable in larger plots, as small-scale variations tend to average out. With regard to plot species richness, Brownstein et al. (2012) found this factor (alpha diversity, Whittaker 1960) had no influence on stochasticity in species composition, although an increase was observed with the community pool size (gamma diversity, Whittaker 1960). Finally, by influencing the differentiation of the world's major biomes and vegetation types (Loidi et al. 2022), climate variables are likely to be important drivers of baseline turnover. Stochasticity may be strongly related to the particular characteristics of the respective vegetation type, so we expected to find a significant influence of climate variables, with fluctuations probably greater in areas with a continental climate, characterised by large seasonal differences (Bakker et al. 2023).



Box 5.1: Conceptual framework of the three components underlying observed changes in vegetation over time. Methodological artefacts under 2) may be avoided by using appropriate methodology. Since the focus of this study is component 3), i.e. "Baseline turnover", we aimed to minimise the influence of components 1) and 2). This was done by introducing the following data-prerequisites: vegetation and environmental stability during the observation period to minimise the first component; and the presence of permanently marked plots, together with experienced botanists carrying out the sampling to minimise second component. It is important to note that baseline turnover will be driven not only by stochastic fluctuations, but also by unavoidable variations, e.g. in plant phenology and observer estimations.

5.2 Methods

5.2.1 Data collection

A total of 57 datasets were gathered, consisting of 3,656 single plots taken from the LOTVS database (Sperandii et al. 2022), the biodiversity exploratory project (Schäfer et al. 2017; Schäfer et al. 2018), public data (Berendse et al. 2021) and provided by individual contributors, following a call for datain the IAVS Bulletin 2021/2 (IAVS 2021). The majority of datasets come from the temperate zone, particularly from North America and Europe. Unfortunately, we were unable to obtain any datasets from the tropics (Figure 5.2). Individual dataset size ranged from 2 to 350 plots, with time series ranging from 5 to 87 consecutive years. The 28 datasets provided by data contributors consisted of complete plot-based vegetation surveys of permanently marked plots, 25 of which included species cover values and the remaining 3 including only presence-absence values. Data from the 29 LOTVS datasets was provided only as previously calculated dissimilarity indices, without any information on species identity. Vegetation sampling was performed annually during a period of at least five consecutive years.

In order to minimise the component of directional change (Box 5.1), the first pre-requisite was that during the observational period no obvious changes had occurred either in environmental conditions (e.g. fire or tilling) or in the vegetation successional state. Slower-acting effects, such as climate change, cannot be ruled out, although these are expected to be of minor importance over the sampling period. The second pre-requisite was that data derived exclusively from permanently marked plots (i.e. not only relying on plot coordinate data) in order to avoid pseudo-turnover due to relocation error and that sampling was carried out by experienced botanists.

For all plots, available meta-data covered the vegetation type, location, plot size, and median species richness over time. Plot size ranged from 0.01 m^2 to 400 m^2. Three datasets provided different plot sizes within the same project. Most time series were collected by the same person. Species richness data was available for all plots as median plot richness over time. The size of the regional community pool, i.e. the number of species occurring at least once in the respective dataset over the whole sampling period, could only be calculated for those 28 datasets that have not been provided as previously calculated dissimilarity matrices. Additional information on the life span of species (annual/perennial) was gathered from several databases: the LEDA database (Kleyer et al. 2008) and Floraweb (BfN 2021) for Europe; the PLANTS database (USDA, NRCS 2022) for North America; and the Austraits database (Falster et al. 2021) for Australia. For South African and Brazilian species, we relied on the expert knowledge of co-authors. For each dataset, the following climate data was gathered: mean annual temperature and precipitation, together with annual seasonality of temperature (expressed as standard deviation · 100) and precipitation (expressed as the coefficient of variation: the ratio of standard deviation / mean). Data was extracted from

WorldClim version 2.1 (Fick & Hijmans 2017) based on plot coordinates. Köppen-Geiger climate classifications for the present day (1980–2016) were extracted from Beck et al. (2018). Detailed information on the data sources and their characteristics can be found in Table A14 in the Appendix.

For the purpose of comparison, the datasets were clustered into nine broad vegetation types, using the information provided by the dataset owners and the Köppen-Geiger climate classification: 1) deciduous forest understory (6 datasets with a total of 140 plots); 2) evergreen forest understory (2 / 27); 3) semi-natural temperate grassland kept open by management (16 / 890); 4) steppe / prairie vegetation (8 / 318); 5) succulent desert vegetation (2 / 124); 6) desert vegetation (15 / 809); 7) dune vegetation (5 / 772); 8) alpine vegetation (2 / 15); and 9) mire vegetation (1 / 22). All forest and temperate grassland datasets come from cold or temperate climate zones, mostly from those without a dry season. Only species from the shrub and herb layer were taken into account, omitting the tree layer on account of its very slow turnover.

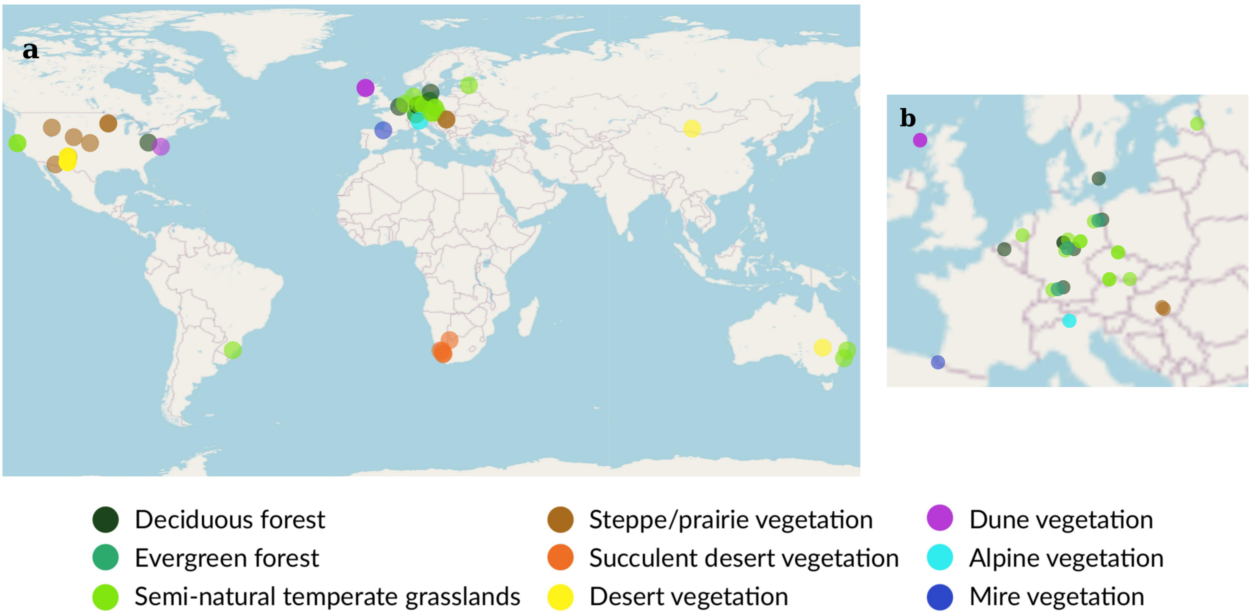


Figure 5.2: a) Sampling locations of all datasets. b) Detailed map for Europe. Darker coloured points indicate overlapping datasets. Basemap: OpenStreetMap.

5.2.2 Data analysis

For each plot, one baseline turnover value was calculated following a two-step process. First, pairwise dissimilarity indices between all available sampling years were calculated per plot. Four indices were employed (Sørensen, Jaccard, Simpson, Hellinger; see Table A13 for definitions), all of which are widely used in vegetation science. They represent different approaches to calculating dissimilarity between plot-based vegetation samples and all have their justifiable uses (see, e.g. Legendre & De Cáceres 2013).

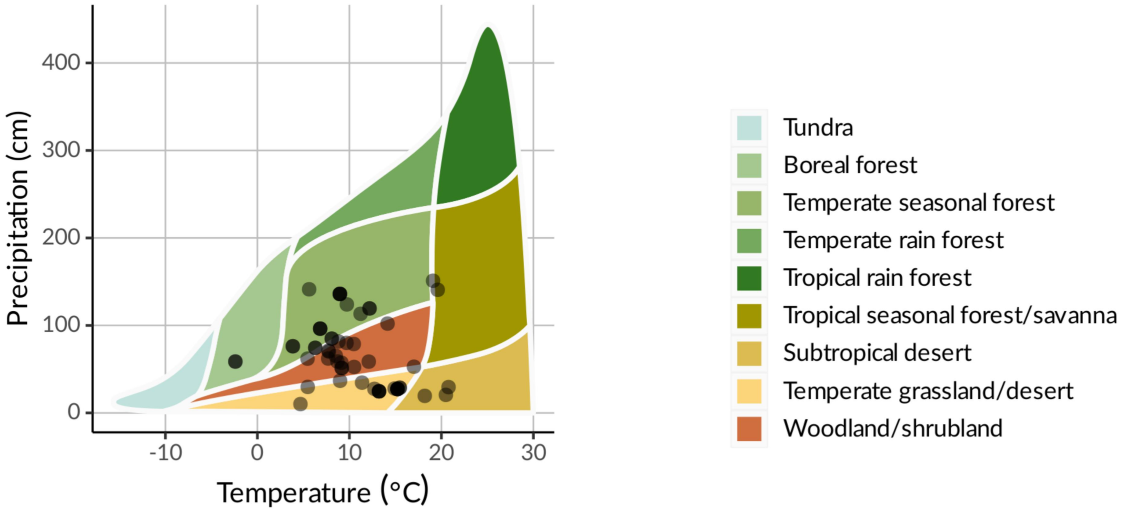


Figure 5.3: Biome classification according to Whittaker (Ricklefs 2008) reporting all collected datasets. Temperature and precipitation values represent mean annual temperature and total annual precipitation taken from WorldClim 2.1 (Fick & Hijmans 2017) for the years 1970–2000.

For each index, calculations were carried out on both presence/absence data and square-root transformed cover data to reduce the weight of highly abundant species, resulting in a total of eight dissimilarity indices. The Hellinger distance, which equals the chord distance calculated on square-root transformed abundance data, was calculated by computing the Euclidean distance on square-root transformed, vector-normalised data to avoid double zero symmetry and reduce the weight of highly abundant species (Legendre & De Cáceres 2013). It is important to note that Simpson dissimilarity (also called the "Lennon index") should not be confused with the Simpson diversity index. The former represents the pure replacement aspect of dissimilarity, as opposed to the richness driven component of dissimilarity (Simpson 1960; Baselga 2010).

Calculated dissimilarity values were then used to construct one logistic model for each plot with dissimilarity values as response variables between 0 and 1. The temporal distance (years) between two samples of the same plot was considered as the independent variable. As logistic models do not allow for values greater than one, Hellinger distances were transformed from their original range of 0–$\sqrt{2}$ to the range of 0–1 by ranging. The intercept value of these models – the "nugget" sensu Brownstein et al. (2012), i.e. the remaining amount of dissimilarity at null temporal distance ($x = 0$) – was back-transformed to dissimilarity values from the logit given by the GLM and taken as the estimate of baseline turnover for the respective plot (example illustrated in Figure A5). The maximum temporal distance used on the x-axis was four years, based on the maximum length of several datasets. This time frame was used in order to ensure that the calculated slope and intercept values between datasets with shorter and longer time series could be compared. For time series with more years available, dissimilarity indices from all sampled years were still used, only pairings with more than four years in between were omitted. The slopes of the models tended to flatten out as more years were added, which tended to yield higher baseline turnover values. The values presented here are, therefore, conservative estimates.

To assess the influence of potential drivers on baseline turnover, we computed four sets of models with baseline turnover serving as the response variable, two of which including one predictor variable (simple (mixed) models) and the remaining two including several predictors (multiple mixed models, Table 5.1). The saturation of plots with species from the community pool was calculated as the ratio of median plot richness (over the observation period) to community pool size, i.e. the total number of species occurring in the respective dataset (Srivastava 1999). To account for the fact that datasets include different numbers of plots sampled over different periods of time, the size of the community pool had to be standardised. The smallest dataset comprised 25 recordings (5 plots × 5 years), in which the community pool size simply consisted of all species present in the dataset. Correspondingly, for all other datasets, 25 random recordings were drawn, and their total number of species counted. This was repeated 1000 times, with the median of the repetitions then yielding the dataset community pool.

The first set of simple models used median species richness and median share of annual species as predictors of within-dataset baseline turnover variation, calculated separately for each dataset using binomial generalised linear models. For the second set of simple models, data points from all datasets were merged, i.e. baseline turnover was modelled across all plots. Here we employed generalised mixed models from the binomial family to account for the correlation structure, with dataset as the random factor (package lme4, Bates et al. 2015). To visualise the results of the mixed models, the function "ggpredict" (Lüdecke 2018) was used to plot the study-level effects of the predictor variables.

Two sets of multiple models were constructed to compare the effect size of the different predictors. One set included the proportion of annual species as well as species saturation as predictors and the other excluded them, since these variables were only available for approximately half of the sampled plots (Table 5.1). Correlations between predictor variables were assessed with a Spearman rank correlation test (Figure A6). Some were expected, such as species richness and the community increasing pool on larger plots. Climate variables were mainly correlated with each other. In addition, the percentage of annual species increased with the seasonality of precipitation and species richness was greater at higher precipitation values and low annual temperature variation. Some correlations do not have a plausible ecological background and are probably best explained by the specific structure of the collected data. For example, the proportion of annual species increased with plot size, which is an artefact related to datasets gathered in regions with more annual species that also happened to be those with large plots.

Table 5.1: Overview of the model setup. "Baseline turnover", based on the respective eight dissimilarity indices, was always the response variable. "p/a" = presence/absence.

Model set	**Simple 1 – within datasets**	**Simple 2 – across datasets**	**Multiple 1 – with all predictors**	**Multiple 2 – with all plots**
Model technique	generalised linear models (glm) from the binomial family (logistic models)	generalised linear mixed models (glmer) from the binomial family (logistic models), dataset as a random factor		
Predictors	- median species richness - median share of annual species	- median species richness - median share of annual species - plot size - size of the community pool - species saturation - mean annual temperature - annual precipitation - seasonality of precipitation - seasonality of temperature	- median species richness - median share of annual species - plot size - species saturation - mean annual temperature - annual precipitation - seasonality of precipitation	- median species richness - plot size - mean annual temperature - annual precipitation - seasonality of precipitation
n (plots = data points per model)	dependent on dataset size: 3–300	dependent on predictor: - 3148 (median species richness, plot size, climate variables) - 1622 (community pool, species saturation) - 1622 (median share of annual species) - 1488 (median share of annual species cover)	1622 (p/a based indices) 1488 (abundance based indices)	3558 (p/a based indices) 3390 (abundance based indices)
n (models)	dependent on data availability per predictor: 428 (species richness) 172 (share of annuals)	9 (predictors) × 8 (response variables) = 72	8 (response variables)	8 (response variables)

All predictors which were used together in the same model had a variance inflation factor (VIF) below 5. The variables "seasonality of temperature" and "community pool size" were not included in the multiple models due to strong correlations with other variables. Predictors were standardised to zero-mean and unit-variance prior to model construction to make their effects comparable. Model selection was performed by running model variants with all possible predictor combinations and ranking them according to the Akaike information criterion (AIC) using the "dredge" function (Bartoń 2022). The model with the lowest AIC and those models within two units of the top model are reported in the Results section (Burnham & Anderson 2002).

All data analyses were performed in R version 4.3.1 (R Core Team 2022) and RStudio (RStudio Team 2022), with the packages *car* (Fox & Weisberg 2019), *data.table* (Dowle & Srinivasan 2023), *dplyr* (Wickham et al. 2022), *ggpubr* (Kassambara 2023), *ggplot2* (Wickham 2016), *ggeffects* (Lüdecke 2018), *lme4* (Bates et al. 2015), *MuMIn* (Bartoń 2022), *plotbiomes* (Stefan & Levin 2022), *readxl* (Wickham & Bryan 2023), *scales* (Wickham & Seidel 2022), *stringr* (Wickham 2022), *vegan* (Oksanen et al. 2022), and *viridis* (Garnier et al. 2021).

5.3 Results

Levels of baseline turnover differed substantially across the eight vegetation types which included more than one dataset (i.e. mire vegetation was excluded) (Figure 5.4). The reported specific values cited below refer to the Sørensen index, based on presence/absence data, as this is a well-known, commonly used index. Concrete values for the other indices are given in Table A15. Desert vegetation had the highest amount of baseline turnover across all indices (Figure 5.4, Figure A7–A13), with a mean of 0.41 for the presence/absence-based Sørensen index; the 75 % percentile even extended to 0.47. For all presence/absence-based indices, steppe and prairie vegetation had the second highest dissimilarity values, with a mean of 0.29. Succulent desert vegetation exhibited much lower levels of baseline turnover (mean 0.24) than deserts dominated by other growth forms. Semi-natural temperate grasslands showed a mean value of 0.17. The two temperate forest types, evergreen and deciduous, both had a mean baseline turnover slightly above 0.1, while alpine vegetation showed the lowest baseline turnover value (mean 0.04). Overall, baseline turnover based on different dissimilarity indices showed similar patterns, as can be seen from the high correlation coefficients in Figure A14. The absolute values of baseline turnover depended on the dissimilarity index used, with the Simpson index, by definition, scoring lower values and the Hellinger index exhibiting higher values than the Sørensen index. For Sørensen, Jaccard and Simpson dissimilarity indices, the abundance-based version generally yielded higher values than the presence/absence-based version, most notably in semi-natural grasslands and dune vegetation (Figure 5.4, Figure A7–A13). Steppe/prairie vegetation was the exception here, where baseline turnover based on species frequency was higher than than the cover-based version. Furthermore, no notable differences for desert vegetation were observed. The replacement component in total turnover (i.e. the Simpson index divided by the Sørensen index) amounted to an average of 0.56 and 0.63 for presence/absence-based indices and abundance-based indices, respectively (mean of dataset means, Figure A15, Baselga 2010). At higher levels of baseline turnover, replacement played an increasingly important role (Figure A16). Detailed values for each dissimilarity index, vegetation type, and dataset, together with the corresponding environmental data, are reported in Table A14 and A15.

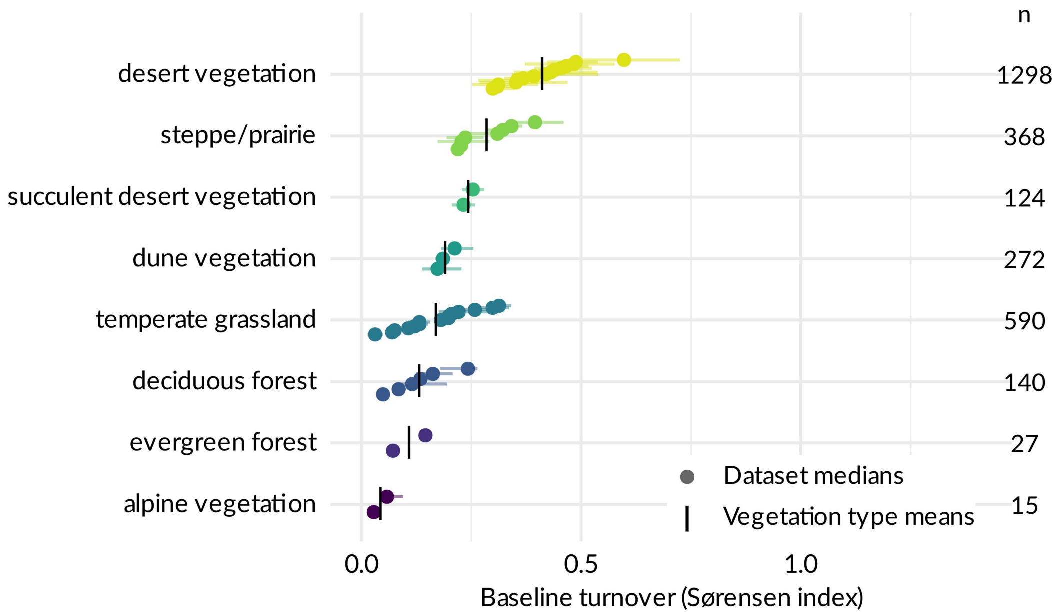


Figure 5.4: Levels of baseline turnover in eight different vegetation types. Baseline turnover is expressed using the Sørensen dissimilarity index based on presence/absence data; medians and 25 %–75 % quantile ranges are displayed per dataset, together with vegetation type means. Plots smaller than 0.25 m^2 and the vegetation type “mire” (with only one dataset) are omitted from this data summary. See Figure A7–A13 for corresponding results for the remaining seven dissimilarity indices.

5.3.1 Drivers of baseline turnover

Patterns within datasets

A direct comparison between baseline turnover in plots with different sizes was possible for three datasets that had sampled plots with different dimensions within the same sites. Baseline turnover clearly increased with decreasing plot size, although to varying degrees (Figure 5.5). In deciduous forest, a 25-fold plot size reduction resulted in an increase in baseline turnover of 135 % (Sørensen index), while the (proportionally) same plot size reduction in dune grassland led to an increase of 138 %. In contrast, in the semi-natural temperate grasslands the increase in baseline turnover amounted to only ca. 68 % for a 100-fold decrease in plot size.

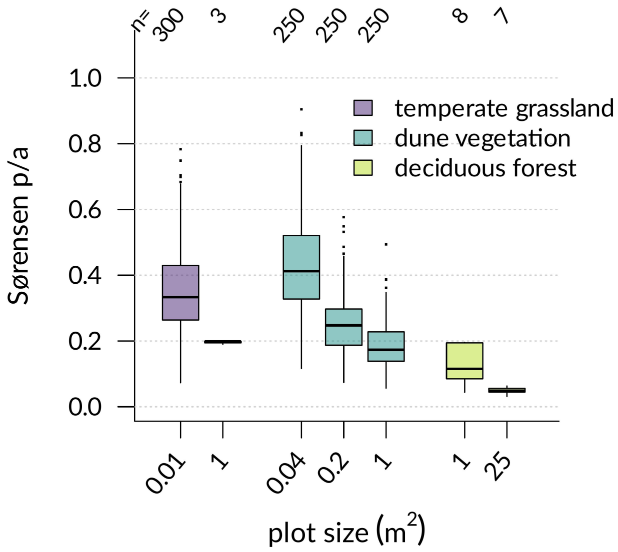


Figure 5.5: Baseline turnover in three datasets which provided different plot sizes within the same projects. Baseline turnover (expressed using the Sørensen index based on presence/absence data) increased with decreasing plot size in all three datasets.

Weak effects of species richness and proportion of annual species on baseline turnover were found within datasets, i.e. within the same habitat, plot size and community pool size. Across all datasets, 59 % of models had positive estimates for species richness and 72 % had positive estimates for the proportion of annual species, meaning baseline turnover tended to increase as the percent of annual species increased. However, there were no significant results after p-value correction for multiple testing (Table A16, A17).

Patterns across datasets

Baseline turnover was influenced by climate variables. There was a positive relationship between mean annual temperature and baseline turnover for all eight dissimilarity indices, while an increase in rainfall resulted in a lower baseline turnover for six indices (Figure 5.6, Figure A17–A23). Greater seasonal differences in precipitation also led to significantly increased baseline turnover across all datasets, while the effects of temperature seasonality were weak. A positive relationship between the proportion of annual species and baseline turnover was found for four out of the eight indices, together with a negative relationship between plot size and baseline turnover. Higher median plot species richness led to reduced baseline turnover for six indices. A significant negative effect of saturation with species from the community pool was also found for seven out of the eight indices, indicating that less saturated plots exhibit greater magnitude of stochasticity in their species composition. Community pool size alone, however, was never found to influence baseline turnover. Backwards selection from a full model in Model set 1 (i.e. models including all available predictors) revealed that, in descending order, the following variables were the most influential drivers:

species saturation, plot size, the proportion of annual species, mean annual temperature and species richness (Table 5.2). The direction of influence remained the same as that found in the simple models for these predictors. For Model set 2, excluding species saturation and the proportion of annual species, mean annual temperature, plot size, and annual variation in rainfall remained most frequently in the final models (Table 5.2).

5.4 Discussion

This study provides first estimates of the amount of stochasticity in species composition change for nine ecosystems, aiming to disentangle noise from signal in the observation of vegetation dynamics. Results may help vegetation ecologists when interpreting the outcomes of resurvey studies which are focused on measuring directional change.

5.4.1 Drivers of baseline turnover

Plot size was found to have a negative influence on baseline turnover, both within and among datasets (Figure 5.5 and Figure 5.6, respectively), while also remaining an important predictor in the final multiple models (Table 5.2). This is in line with the literature showing how the role of chance in species assembly is strongly dependent on the spatial scale selected to investigate plant communities (van der Maarel & Sykes 1993; Nekola & White 1999). Large plots allow more species to co-exist and result in less randomness in terms of which species will appear at a given time (van der Maarel & Sykes 1993). The amount of chance could, therefore, be reduced when sampling larger plots since these are more likely to include rare species. Moreover, edge effects for immigration or emigration in large-sized plot would also be reduced. Said this, we are aware that plot size in vegetation studies is usually chosen on the basis of a trade-off between reliability and practicality; this is the reason why we are interested in the amount of chance recorded at the most commonly used scales. This allows for a comparison of estimates to be made between this and other studies, which should always take into account sampling size. Overall, our results suggest that larger plots may have an advantage over smaller plots when carrying out studies of directional change as the amount of random fluctuation is reduced.

Plot-level species richness, community pool size, and saturation with species from the community pool are all naturally related variables, and were found to be correlated with plot size (Figure A6).

Species saturation was the most influential driver in the optimised multiple models, with baseline turnover decreasing as saturation increased. This variable was largely independent from the community pool size (Spearman's ρ: 0.06) and was only weakly correlated with plot size (Spearman's ρ: 0.18). Consequently, species saturation results as the most informative of the three richness-related metrics regarding species richness dynamics and baseline turnover. Chave (2004) and Lieberman & Lieberman (2007) postulated that, in more species-rich communities, there would be a greater redundancy of species which can potentially fill a particular niche, leading to increased stochastic processes of community assembly. Lower species saturation levels can be seen as an indicator of higher redundancy and may, therefore, lead to increased baseline turnover, i.e. greater stochasticity.

Higher plot-level species richness alone significantly reduced baseline turnover. However, when this variable remained in the multiple models, the direction of baseline turnover was the opposite, being mostly positive. The correlation of species richness and plot size might provide a possible explanation of this pattern: the negative effect of species richness on baseline turnover in the simple models is probably due to simultaneously increased plot size – plot size being the most important driver in the multiple models. When combined in the multiple models, the positive model estimates of species richness converge with findings from spatial analyses by Brownstein et al. (2012) and the theoretical idea that the results of species interactions and competition may become increasingly random with an increasing species pool size (Pool 1989; Fowler 1990; Hubbell 2001).

In contrast with the results from spatial analyses in Brownstein et al. (2012), baseline turnover was not influenced by community pool size. However, the effect of this variable might have been masked by plot size: increasing plot size led to reduced baseline turnover and, at the same time, to a larger species pool. This means that a potential increase in baseline turnover with increasing community pool size (following the previously illustrated theory) may have been overridden by the effect of the spatial scale.

Baseline turnover was, on the other hand, influenced by climate variables, with the mean annual temperature being the principal driver and, in some cases, the sum and seasonality of annual rainfall also remaining in the optimised multiple models (Table 5.2). In the simple models (Figure 5.6), baseline turnover similarly increased with higher temperatures, less rainfall and greater rainfall variability over the year. Regular drought events in warm, dry regions with high seasonality may act as disturbance factors, which have been found to increase stochasticity in community assembly (Kreyling et al. 2011).

The role of annual species was also found to be important in both the simple (Figure 5.6) and multiple models (Table 5.2), the reason for this being straightforward: the occurrence of annuals naturally fluctuates from year to year, easily disappearing or reappearing within short periods of time in a limited space such as a vegetation plot. Consequently, community assembly processes are more prone to stochastic events. This is probably linked to the influence of climate on the life form of dominant species. Since there was a correlation between the proportion of annual species with climate variables in the same way as with baseline turnover, we are probably seeing an indirect effect of climate on baseline turnover, mediated by the success and proportion of annual species.

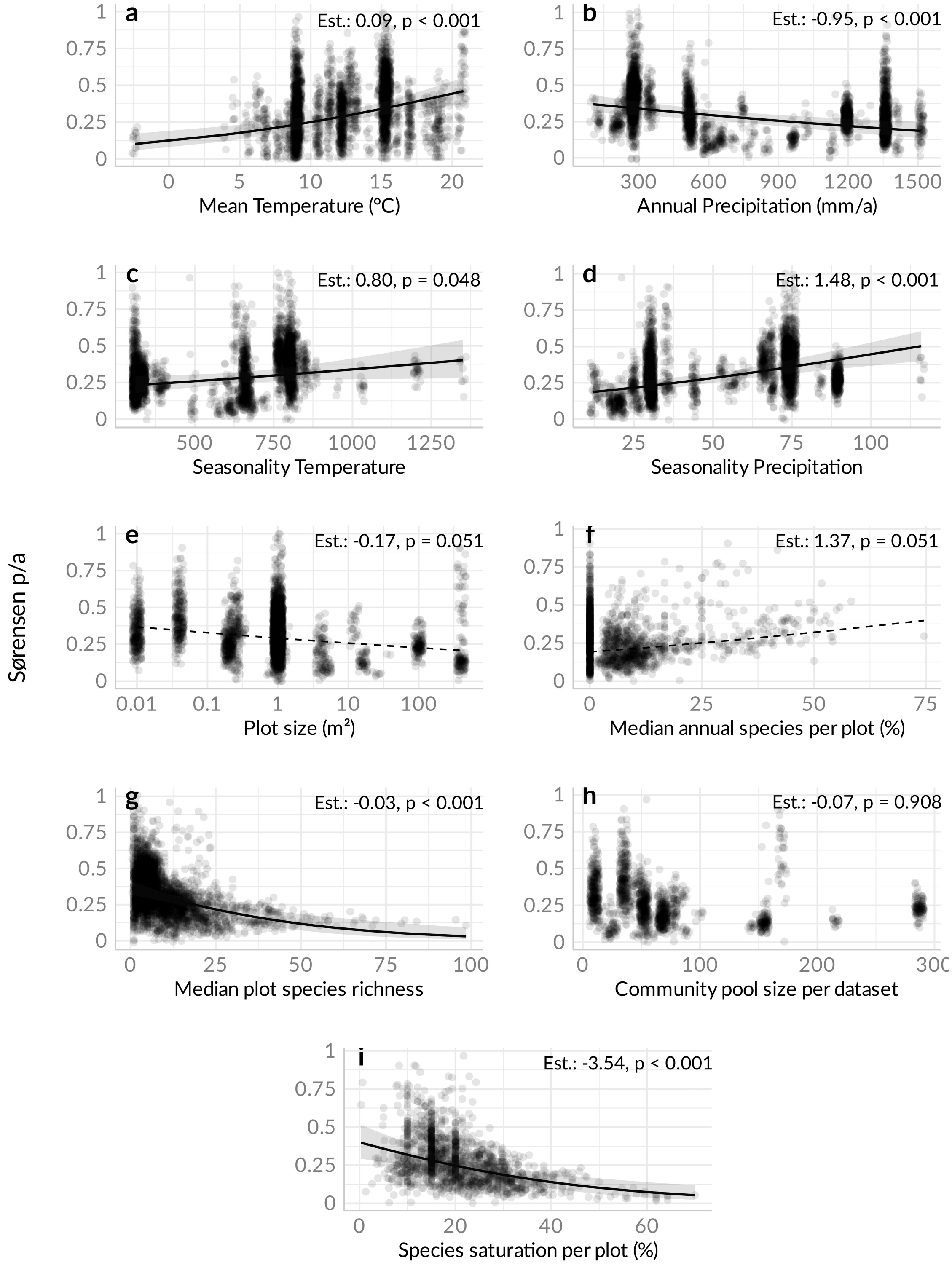


Figure 5.6: Simple mixed models showing the relationship between baseline turnover expressed using the Sørensen index based on presence/absence data and (a) mean annual temperature, (b) mean annual precipitation, (c) temperature seasonality (d) precipitation seasonality, (e) plot size (logarithmic scale), (f) median proportion of annual species per plot, (g) median species richness per plot, (h) community pool size, (i) species saturation per plot (median species richness/community pool). Trend lines represents results o‘f logistic models at the population level (function “ggpredict”); dashed lines indicate significance levels between 0.05 and 0.1; strongly overlapping data points made visible by jittering (subplots a–e, h). See Figure A17–A23 for corresponding results for the remaining seven dissimilarity indices.

Table 5.2: Summary of the final multiple mixed logistic models, following model selection, for baseline turnover expressed using eight dissimilarity indices. The reported final models are those with the lowest AIC and those within two units of the top model; dataset was used as a random factor in all models. Symbol/colour coding: +/green, positive effect of the predictor (columns); –/red, negative effect of the predictor. Numbers in brackets represent the percentage of final models in which the predictor remained. Results are presented from both sets of multiple models, one including all predictors (Model set 1, $n_{p/a} = 1622$, $n_{abund} = 1488$) and one excluding the proportion of annual species and species saturation (Model set 2, $n_{p/a} = 3558$, $n_{abund} = 3390$, see Table 5.1). "n.a."= respective predictor not included in the full model; "p/a" = presence/absence-based version of the index. See Table A18 for detailed model coefficients.

	Saturation	**Plot size**	**% Annual species**	**Mean temperature**	**Species richness**	**Seasonality rainfall**	**Annual rainfall**
Model set 1							
Sørensen p/a	–(100)	–(100)	+(83)	+(83)	+(17)	–(17)	–(17)
Sørensen abundance	–(100)	–(100)	+(88)	+(50)	+(75)	+(12)	–(38)
Jaccard p/a	–(100)	–(100)	+(100)	+(100)	+(25)	–(25)	–(25)
Jaccard abundance	–(100)	–(100)	+(86)	+(71)	+(71)	+(14)	–(14)
Simpson p/a	–(100)	–(100)	+(83)	+(83)	+(17)	–(17)	+(17)
Simpson abundance	–(100)	–(100)	+(100)	+(20)	+(80)	–(20)	+(20)
Hellinger p/a	–(57)	–(38)	+(71)	+(90)	+-(14)	+(29)	+(19)
Hellinger abundance	–(46)	–(50)	+(67)	+(67)	+(17)	+(42)	+(4)
Model set 2							
Sørensen p/a	n.a.	–(100)	n.a.	+(100)	–(50)	+(50)	–(100)
Sørensen abundance	n.a.	–(100)	n.a.	+(100)	+(25)	+(75)	–(75)
Jaccard p/a	n.a.	–(100)	n.a.	+(100)	–(25)	+(75)	–(75)
Jaccard abundance	n.a.	–(100)	n.a.	+(100)	+(33)	+(100)	–(33)
Simpson p/a	n.a.	–(86)	n.a.	+(100)	–(43)	+(29)	–(43)
Simpson abundance	n.a.	–(100)	n.a.	+(100)	+(25)	+(25)	+(25)
Hellinger p/a	n.a.	–(75)	n.a.	+(100)	+(25)	+(100)	–(25)
Hellinger abundance	n.a.	–(80)	n.a.	+(100)	+(60)	+(20)	–(20)

5.4.2 Comparing estimates and limitations

Regarding baseline turnover estimates, ranges were well matched with similar vegetation types in the regional study based on spatial analyses by Brownstein et al. (2012). The values for montane grassland in Brownstein et al. (2012) (0.16–0.18) fit within baseline turnover rates from temperate montane or poor grasslands in our analysis (0.06–0.19, Table A15). Two forest types from Brownstein et al. (2012) (nugget 0.14–0.31) were also similar to our baseline turnover estimates for temperate forests (mean 0.21), despite geographical differences in the collected data. In the two remaining forest types, values of Brownstein et al. (2012) exceeded ours (0.42–0.58), while plot size was comparable.

The time series in the present study cut off well before the saturation point of the logistic curves, in a trade-off between being able to use more datasets and having longer time series. This results in a certain amount of uncertainty in the reliability of estimated intercepts. Since the study by Brownstein et al. (2012) does not suffer from this limitation, the congruencies in results illustrated above are reassuring. In comparing the values directly, we assume that the dimension, space or time, should not matter if it is reduced to zero, leaving only the component of chance to explain differences in species composition. Furthermore, it is important to note that while the present data collection features datasets from a wide range of vegetation types worldwide, they are not all equally well represented. In particular, the results for alpine vegetation, succulent desert vegetation, and evergreen forest should be interpreted with caution as they are each based on only two datasets. Additional data is, therefore, required to further consolidate the results presented here. Lastly, we were unable to cover all relevant vegetation types, with data for tropical vegetation or savannah, for example, not represented at all.

5.4.3 An application example

One example of a potential application can be taken from a meta-analysis of resurveyed grasslands (Diekmann et al. 2019), where six datasets of dry grasslands resurveyed after a span of 16 to 78 years were collected. The authors report that presence/absence-based pairwise Jaccard dissimilarities between original and resurveyed plots had an average dissimilarity of 0.642 (max. 0.773, min. 0.462). In our study, the median baseline turnover for semi-natural temperate grasslands is 0.27 for the Jaccard index, with the 25 % and 75 % percentiles ranging from 0.25 to 0.30 (Table A15, Figure A8). More specifically, for the four semi-natural grassland datasets that were classified as “dry grasslands”, the median is 0.27 (0.19–0.33, Table A15). When compared to estimates reported by Diekmann et al. (2019), baseline turnover makes up for less than half of the dissimilarity in species composition found after a longer time span in these vegetation types. The authors can therefore be confident that the trends found in their resurvey study represent more than just random fluctuation, meaning that actual directional change has been observed.

5.5 Conclusion

We introduced the concept of baseline turnover as an estimate of the component of chance in species composition dynamics based on time series data. In the current study, first estimates of baseline turnover are presented for nine vegetation types worldwide. The magnitude of baseline turnover was found to be in line with commonly observed values of methodological pseudo-turnover, making this a relevant factor to consider in the ongoing challenge of disentangling signal from noise in observed vegetation changes. We urge vegetation ecologists to make a comparison between dissimilarity values obtained in resurvey studies and the presented thresholds for baseline turnover so that the abstract value of a dissimilarity index can be better interpreted.

Plot size, species saturation from the community pool, mean annual temperature and the life span of occurring species were identified as the main factors driving baseline turnover. As smaller plots were found to lead to higher stochasticity in community composition, we suggest that researchers avoid using small sampling units in studies of vegetation dynamics so that directional dynamics are not masked by the component of chance.

5.6 List of Appendices

Figure A5: Illustration of the calculation of baseline turnover.
Figure A6: Scatterplots and correlation coefficients between all predictor variables.
Figures A7–A13: Levels of baseline turnover in eight different vegetation types, expressed as the additional seven dissimilarity indices.
Figure A14: Scatterplots and correlation coefficients between baseline turnover values based on the eight used dissimilarity indices.
Figure A15: Share of replacement in total turnover for presence/absence and abundance-based calculation of indices, respectively.
Figure A16: Share of replacement in total turnover.
Figures A17–A23: Simple mixed models showing the relationship between baseline turnover expressed using the remaining seven dissimilarity indices.
Table A13: Computation formulae of the eight dissimilarity indices.
Table
Table
Table A16: Model results regressing baseline turnover against the median species richness of the respective.
Table A17: Model results regressing baseline turnover against the mean share of annual species of the respective.
Table A18: Detailed model estimates of multiple mixed logistic models.

5.7 Acknowledgements

We would like to thank the participants of the 64th IAVS symposium in Madrid for the fruitful discussions which led to considerable improvements in the methodology and Peter Adler as well as the late Hartmut Dierschke and Germund Tyler for contributing to the data collection.

5.8 References

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— Chapter 6 —

Synthesis

Mesic Arrhenatheretum meadow (Arrhenatherion elatioris Braun 1915) on chalk-poor soil with *Holcus lanatus*, *Anthoxantum odoratum*, *Cynosurus cristatus*, and *Saxifraga granulata*. Roßbach, Hesse, Germany, 2020.

Grasslands are highly biodiverse habitats that depend largely on human management practises in Europe. Their extent and characteristics are severely threatened by changes in land use, resulting in a significant loss of biodiversity (Dengler et al. 2014). Resurvey studies are an effective tool for monitoring long-term changes in species composition and diversity (Bakker et al. 1996). With the increasing availability of historical vegetation surveys, they have gained popularity in the last decades, allowing for many insightful studies (Hédl et al. 2017). However, grasslands are under-represented in these studies. The contributions of this thesis are twofold – first, two resurvey studies were conducted to contribute to the body of knowledge about biodiversity change in grasslands, and second, a statistical and a new theoretical concept were introduced to improve the methodology of resurvey studies. In this synthesis, we summarise the findings of the two case studies of different grassland types (Chapters 2 and 3) and relate them to practical nature conservation issues. The results of these resurveys are then reflected with regard to common methodological uncertainties. We apply the theoretical concepts developed in this thesis (Chapters 4 and 5) and discuss their implications for the interpretation of resurvey studies.

6.1 Resurvey case studies

The two case studies of resurveys in this thesis were conducted on different types of grasslands, with varying time spans between the initial and the follow-up surveys. The first resurvey on *Nardus* grasslands in the Eifel mountains (North Rhine-Westphalia, Germany) was carried out in 2018, 32 years after the initial study. During those, a continuous management took place after the sites had previously lain fallow. The focus of this study was therefore to examine the impact of management under the influence of ongoing environmental stressors, such as atmospheric deposition and climate change. Remnant wet heath stands in the region were subject to the same management and environmental conditions and were also included in this resurvey. The second resurvey of calcareous grasslands in Lower Saxony, Germany, was performed in 2019, eleven years after the initial survey. These years were exceptionally dry, so the focus here was on the impact of the drought on the vegetation. As periods of drought during the growing season are likely to become more frequent in the future due to climate change (IPCC 2014), the aim was to investigate the sensitivity of this species-rich grassland type to climate change.

6.1.1 Resurvey *Nardus* grasslands and wet heaths

Our resurvey confirmed findings of soil pH recovery over recent decades, which has been even more pronounced than in other German regions (Peppler-Lisbach et al. 2020). The general trend of eutrophication, replacing specialised and characteristic species with more general and nutrient-demanding species, was only weakly present in the Eifel. This can be attributed to the exceptionally consistent management regime of yearly mowing for the past

30 years. It also led to an increase in species adapted to low nutrient levels, but not to low pH values. However, the same management regime was not appropriate for the conservation of the wet heaths in the area.

State of knowledge – Trends in *Nardus* grasslands

The loss of *Nardus* grasslands since pre-industrial times is mainly caused by the abandonment of common land pastures in the low mountain ranges with subsequent afforestation. In addition, where profitable, they have been converted into highly productive grassland through melioration, i.e. fertilisation and sometimes drainage (Peppler-Lisbach & Petersen 2001; Schwabe et al. 2019). For example, a loss of 85–96 % of the area of *Nardus* grasslands in the Black Forest between the 1950s and 1980s was documented by Hobohm & Schwabe (1985). Generally, *Nardus* grasslands had a higher melioration potential than other nutrient-poor grassland types because of their usually good water supply (Peppler-Lisbach & Petersen 2001). As a result, out of 79 species listed by Ellenberg et al. (1992) as character species of *Nardus* grasslands (group 5.1.1 – *Nardetalia*), 72 % are currently included as threatened in the Red List of Germany (Metzing et al. 2018).

There are five recent resurvey studies of *Nardus* grasslands, with a focus on Germany (Peppler-Lisbach & Könitz 2017 (North Hesse); Peppler-Lisbach et al. 2020 (North Hesse & Rhön); Schwabe & Kratochwil 2021; Schwabe & Kratochwil 2022 (both Black Forest)) and one additional study from the UK (Mitchell et al. 2017). The initial recordings of those five studies were carried out between 1958 and 1987, and the follow up surveys were conducted from 2012 to 2021. Overall, total species richness did not show significant trends, but the species composition changed towards more nutrient-demanding and acid-sensitive species in all studies, though to a lesser extent in the high-montane Black Forest (Schwabe & Kratochwil 2022). In all cases but the high-montane Black Forest, this was accompanied by a decrease in specialist and characteristic species adapted to acidic soils and nutrient-poor conditions. Accordingly, also the mean Ellenberg indicator values for nutrients increased in four out of the five resurveys (except for Mitchell et al. 2017) and mean Ellenberg soil reaction values increased in all studies except Schwabe & Kratochwil (2022). In one case, also species indicative of fallows increased (Peppler-Lisbach & Könitz 2017). Overall, this indicates an ongoing eutrophication of the swards to varying degrees, depending on local soil conditions, management (history), and levels of nutrient deposition. The authors attribute the changes in species composition mainly (i) to a rise in pH values due to the recovery from previous soil acidification by sulphur oxide deposition (Mitchell et al. 2017; Peppler-Lisbach & Könitz 2017; Peppler-Lisbach et al. 2020; Schwabe & Kratochwil 2022), (ii) a lack of management intensity (Peppler-Lisbach & Könitz 2017; Peppler-Lisbach et al. 2020; Schwabe & Kratochwil 2022), and (iii) eutrophication by nitrogen deposition (Peppler-Lisbach & Könitz 2017; Peppler-Lisbach et al. 2020; Schwabe & Kratochwil 2021). Sulphur oxide depositions have had a negative impact on the diversity and characteristic species composition of acid grasslands in the past (Maskell et al. 2010; McGovern et al. 2011). Due to effective environmental regulations, they have declined strongly since the 1990s, leading to a recovery of soil pH values (Mitchell et al. 2018; Peppler-Lisbach & Könitz 2017; Peppler-Lisbach et al. 2020).

A European study of *Nardus* grasslands using data collected between 1939 and 2007 found the same general eutrophication trend (Dupré et al. 2010). Here, the authors additionally observed a decrease in total species richness. They appointed the changes mainly to the influence of atmospheric depositions, especially of nitrogen, and to a lesser extent of sulphur oxide. Especially slow growing, low-competitive herbs were decimated, while grasses tended to profit from the additional nutrient inputs.

Climate change is still considered a subordinate risk factor for *Nardus* grasslands, even though it might gain importance in the future (Stanik et al. 2021). Nonetheless, Behrens et al. (2009) predicted that cold-adapted montane species (e.g. *Arnica montana*) are endangered by warming temperatures due to a lack of "escape" possibilities to higher altitudes.

Another habitat type that was surveyed in this study were wet heaths. They typically grow on wet and acidic soils, occasionally with a peat layer. Its most characteristic species is the cross-leaved heath (*Erica tetralix*), which is often accompanied by *Sphagnum* mosses (Leuschner & Ellenberg 2017). This habitat type is classified as "critically endandered" to "threatened with destruction" in Germany (BfN 2017).

Our results and remarks on conservation practice

The results of our resurvey study on *Nardus* grasslands and wet heaths in the Eifel mountains (Chapter 2), covering the time span between 1986 and 2018, confirmed the general trend of pH increase in acidic soils (Mitchell et al. 2017; Peppler-Lisbach et al. 2020). Signs of eutrophication were also present, albeit to a lower extent compared to the other resurvey studies summarised above. For example, mean Ellenberg indicator values for nutrients and soil reaction stayed stable, at least when weighted by species presence only. They increased significantly when species cover was taken into account. Only the cover of character species had decreased, but not their numbers. This was unexpected, as pH values were found to have increased even more than in north Hesse and the Rhön (Peppler-Lisbach & Könitz 2017; Peppler-Lisbach et al. 2020). The siliceous soils of the Eifel have little buffer potential, so that in the 1980s, the pH values were particularly low due to sulphur oxide deposition. The basaltic and thus better buffered parent rocks of the central German low mountain ranges ensured a less pronounced drop. The strong increase in pH in the Eifel can therefore be interpreted as a recovery from particularly acidified conditions. This has provided an opportunity for acid-sensitive species to invade the swards. Compared to other regions, however, this has occurred at a very low level. More nutrient-demanding species of agricultural grasslands have appeared, but their cover sums have not increased significantly compared to 1985. Instead, more species indicative of nutrient-poor conditions (but not adapted to low pH values) and small sedge fens have been observed in 2018.

The annual mowing over the last 30 years represents a remarkably stable and thorough management that was not carried out in this way in other regions. We believe that this management regime is the reason why the eutrophication processes induced by pH recovery and atmospheric depositions have been stopped or at least slowed down. However, the importance of details in the management practices should not be underestimated. In the present case, these are secured in contracts with local farmers who agreed to mow the swards once a year in exchange for financial compensation for biodiversity-friendly management. This type of agreement is called "contractual nature conservation" and is usually co-financed by the EU. Conditions for this type of agreement are comparably good in the northern Eifel, as contractual nature conservation has a long tradition there. It was here that this concept was first developed under the guidance of Wolfgang Schumacher in the 1980s (Schumacher 2007). Since then, it has proved to be a very effective tool in keeping management practices alive that are no longer economically viable, thereby preserving the vegetation types that depend on them (Schumacher 2013; Leuschner & Ellenberg 2017). One crucial detail is the timing of mowing, which should not be carried out too late in the year, preferably in July (Briemle 2004; Peppler-Lisbach & Fischer 2022). The date is important for the amount of nutrients that can be removed. If plants capable of transferring nutrients from their above-ground biomass to their roots (e.g. *Molinia caerulea*) are given the opportunity to do so in autumn, auto-eutrophication and fallow development cannot be prevented despite the annual management (Briemle 2004). As climate change is moving the vegetation development earlier into the year (Übel 2023) and higher temperatures facilitate nutrient enrichment through increased microbial activity (Liu et al. 2017), even earlier mowing dates may be necessary in the future (Wieden 2004). However, it does not seem to be absolutely necessary to remove biomass every year (Peppler-Lisbach & Petersen 2001; Briemle 2004). Ideally, mowing should be staggered, e.g. to provide nectar and pollen sources for flower-visiting insects over the entire vegetation period (Schwabe et al. 2019). However, as Schumacher (2007) emphasised, it is important that the requirements of contractual nature conservation remain practicable for farmers. Thus, such a specification is probably too ambitious.

Although the separate sites that were surveyed showed common trends, they differed in some respects. This was reflected by the variable "site" explaining the highest amount of variance in the redundancy analysis (RDA, Figure A7). It highlights the strong influence of site-specific idiosyncrasies, such as their land use history, connectivity in the landscape, or chance events (e.g. diaspores reaching the site). For example, although *Molinia caerulea* cover decreased significantly overall, there was one site where it was practically absent in the initial study and where it now has cover values similar to the other sites. Here, the cover of *Nardus stricta* has been reduced to a much larger extent than in the other sites. The southernmost site exhibited a markedly higher increase in nutrient-demanding species compared to all other sites, possibly due to a past fertilisation event that may still be affecting current developments. The landowner and their detailed actions could be a decisive factor in this regard. For example, the type of grassland that is mowed immediately before the *Nardus* grassland can have a significant impact. Mowers can transport seeds of both desired and undesired species (Klinger et al. 2021), which can be detrimental if the previously visited site had many unwanted agricultural grassland species. However, it may also contribute to a small habitat network if the *Nardus* grassland sites were all mowed by the same machine. Unfortunately, this is rather unrealistic here, due to the considerable distances between sites (1.5–4 km) and the fact that almost every site is owned by a different landowner.

In the wet heaths, the same management and overall conditions (i.e. pH recovery, atmospheric depositions, climate change) have led to entirely different results. The three sites that originally contained wet heaths have largely transformed into wet variants of *Nardus* grasslands, small sedge-dominated swards, or wet meadows with signs of eutrophication. In 2018, only remnants of the typical heath species such as *Narthecium ossifragum* or *Trichophorum cespitosum* were found. On average, the cover of *Erica tetralix* had declined by 80 %. This was mainly due to the annual mowing regime introduced in the 1980s, which severely disadvantaged the typical species of wet heaths. Dwarf shrubs such as *Erica* are not able to regenerate as quickly as grasses from regular cutting and have therefore been outcompeted (Leuschner & Ellenberg 2017). As a result, the thicker humus layer created by the slowly decomposing litter of heath species could be decomposed progressively, increasing the available nutrient levels. Recommendations for the management of wet heaths mainly involve short-term, intensive grazing by sheep, possibly accompanied by infrequent topsoil removal in alternating parts of the sites. If mowing is necessary, it should be carried out in a way that resembles top soil removal: only on small parts of the site with several years in between, using low mowers to create open soil patches for heath rejuvenation (NLWKN 2011; BfN 2017). Although wet heaths are considered slow to regenerate (BfN 2017), it may be possible to improve the current conditions for characteristic species with the above measures. However, the remaining sites are very small (at most 0.5 ha) and isolated, making it quite expensive to carry out these steps. Nevertheless, it is important to also maintain suboptimal or small habitats as stepping stones in a habitat network (Pärtel et al. 2005). The present sites are promising as they still have a near-natural water regime and are not adjacent to intensively used areas, thereby avoiding direct influences of fertilisation or drainage. Additionally, there is no dominance by *Molinia caerulea*, which is a common issue in deteriorating wet heaths.

Exkursus on *Arnica*

Arnica montana, the “flagship species” of mountain meadows, showed significant declines in this resurvey study. It is a traditional medicinal plant and listed in the EU Habitats Directive as a species of community interest (Annex V, European Council 1992). In the initial recording in 1986, it was still found in 72 % of plots, while this was only the case in 44 % in 2018. The average cover decreased from 7.5 % to 3 % per plot. A separate survey by

Schumacher et al. (2007) compared the size of the populations in three of our sites between 1990 and 2005. These included the (formerly) largest population of *Arnica* in the NRW part of the Eifel. The results indicated that the populations had increased by 300 to 500 % between 1990 and 2005. Taken together, this result and our findings suggest that we are now seeing the repayment of an "extinction debt" that has built up over the last decades. "Extinction debt" as a concept describes the fact that the effects of habitat deterioration can occur with a time-lag (Tilman et al. 1994). In this case, the conditions for *A. montana* had probably initially improved since the 1990s, due to the decreasing sulphur oxide depositions and the subsequent recovery of pH values, allowing its populations to grow at least until 2005. However, the only form of management for decades has been mowing, resulting in a lack of open soil patches. These patches are crucial for the germination and thus for the generative reproduction of *Arnica* (Richter 2014). Purely vegetative reproduction via stolons means that the stands become overaged over time. As individuals can live for several decades, this process may remain invisible and amount to an "extinction debt" that is payed off when the over-ageing leads to a population collapse (Eriksson 1996; Kahmen & Poschlod 2000).

6.1.2 Resurvey calcareous grasslands

Our study confirmed that particularly warm and dry microclimates generally had a positive effect on the characteristic species composition of dry grasslands in the past (Bennie et al. 2006). However, the changes in vegetation between 2008 and 2019 showed clear signs of the intense droughts of the decade, contradicting experimental studies in which the species composition of semi-arid calcareous grasslands was observed to be robust to droughts (Grime et al. 2008; Maalouf et al. 2012). The microclimatic conditions of the site had an impact on the reaction to drought, with steep, south-facing slopes being more affected. This included a decrease in characteristic species, an increase in ruderal species, and a higher proportion of bare soil.

State of knowledge – (Micro)climate and drought effects on calcareous grasslands

The typical species composition of calcareous grasslands has been found to be promoted by droughts. In drought periods, species that are not adapted to these stressful conditions but might be more competitive, are regularly "sorted out" (Bennie et al. 2006; Leuschner & Ellenberg 2017; Fischer et al. 2020). Droughts may also mitigate the effects of ongoing eutrophication, as limiting soil moisture is known to negatively affect nutrient uptake and thus the competitive ability of fast-growing species (Bennie et al. 2006; Moeslund et al. 2013). These effects can be extended to dry conditions that are not caused by the weather but by microclimatic conditions. Topographically controlled moisture was found to be a key factor in the species composition of calcareous grasslands in the UK (Perring 1959). Species typical of, or restricted to, calcareous grasslands were concentrated on the warmest and driest slopes (steep, Southeast–West), while indifferent or alien species were mainly found on the relatively wetter flat North–Northeast slopes.

Droughts are predicted to increase in frequency and intensity as climate change continues (IPCC 2014). The impact of more extreme droughts on calcareous grasslands is still unclear. On the one hand, species of calcareous grasslands are the best adapted to drought and heat in the Central European landscape, and therefore likely to benefit from a warming climate through an increase in potential habitat area (Behrens et al. 2009; Pompe et al. 2011). On the other hand, an increase in the area of climatically suitable habitat does not guarantee that the species will eventually reach these new sites. Additionally, increasingly frequent and extreme droughts have the potential to threaten the specialised vegetation especially on the most heat-exposed sites (Tilman & El Haddi 1992). To our knowledge, there are only few studies examining the effect of droughts on calcareous grasslands. In a modelling study, an assumed temperature increase of 2 °C was followed by only a slight northward shift of the communities (approx. 100 km, Duckworth et al. 2000). However, the authors acknowledged that this weak response could be due to the model not accounting for changes in precipitation. An experiment with a 13-year summer drought simulation in mesic calcareous grasslands in the UK caused a strong reduction in productivity (-35 %) and a significant decrease in species numbers (Grime et al. 2008). However, shifts in species composition due to the treatment were of lower magnitude than annual fluctuations. Another experiment with induced summer drought did not reveal any significant changes in species composition, even though the total biomass was affected here as well (Grime et al. 2000). Maalouf et al. (2012) found no effects of a two-year simulated spring drought on species richness or Shannon diversity in a mesic calcareous grassland, but significant reductions of both in a xeric grassland. A climate change sensitivity analysis of habitat types under the Habitats Directive placed calcareous grasslands in the highest risk category (Petermann et al. 2007). This was mainly due to their already degraded conditions, limited ability to move to new sites, and susceptibility to neophyte invasion.

Our results and remarks on conservation practice

In the resurvey of calcareous grasslands in Chapter 3, we investigated the effects of microclimate on the species composition and richness of calcareous grasslands in North-West Germany before and during a period of extreme summer drought. The initial vegetation sampling was carried out in 2008, after a period of mostly average precipitation and temperatures (Zink et al. 2016). The period until the resurvey in 2019 was exceptionally dry, with none of the years reaching the long-term median of growing season soil moisture (1951–2008). In 2015, the most extreme summer drought period in Europe for more than 2000 years had begun (Büntgen et al. 2021). The results of the initial recording in 2008 confirmed earlier findings that warmer and drier conditions, as captured in a heat index, had a positive influence on the targeted character species (Bennie et al. 2006; Fischer et al. 2020). In accordance with Perring (1959), more dry grassland character species and fewer nutrient-demanding species occurred on sites with higher heat indices. Accordingly, mean Ellenberg indicator values for nutrients and soil moisture were also lower at higher heat indices. In contrast to drought inducing experiments (Grime et al. 2000; Maalouf et al. 2012), some aspects of the species composition were changed significantly by the dry conditions. The cover of dry grassland character species and number of ruderal species increased, while other grassland species declined. *Bromus erectus*, as one of the two potentially dominant grasses in calcareous grasslands, benefited from the drought, while the other, *Brachypodium pinnatum*, decreased significantly.

The effects of the extraordinary summer droughts differed between sites of different microclimates. Some general effects of the drought were amplified on steep, south-facing slopes, such as a decrease in total vegetation cover, the cover of agricultural grassland species, and the mean Ellenberg indicator for soil moisture. On steep, south-facing slopes, total species numbers, as well as the number of character species and agricultural grassland species, decreased, while they increased on flat and north-facing slopes. This can be interpreted as a warning signal that sites which previously favoured typical semi-arid calcareous grassland species could develop conditions that are too extreme for some typical species under the influence of ongoing climate change. As a consequence, south-facing, steep slopes may no longer be suitable for semi-arid calcareous grassland communities (*Mesobromion* Oberd. 1949) in the future, but may instead harbour xeric communities (*Xerobromion* Br.-Bl. et Moor 1938), as is already the case in southern Germany (Leuschner & Ellenberg 2017). The present plant species will therefore either have to adapt to the new conditions or move to new locations in order to survive (Wiens et al. 2010).

Even in response to gradual climate change, plants are believed to be more likely to move than to adapt (Wiens et al. 2010; Pardi 2012). One way of estimating the extent of range shifts that might become necessary for a species or community to stay in their current climatic niche is through the concept of “velocity of change” (Loarie et al. 2009). In this concept, future environmental conditions are modelled under an assumed climate change scenario. The distance between sites with the same conditions in the present and the modelled future is then related to the time frame in which the environmental change is predicted to take place. Loarie et al. (2009) have estimated the mean global velocity of change for mean annual temperature and rainfall from the year 2000 to 2100 for an intermediate emissions scenario to be 420 and 220 m year^{-1}, respectively. This means that two sites with the same temperature, one in the present and the other one in 2100, are predicted to be, on average, 42 km apart (420 m × 100 years). Species would therefore have to move at an average speed of 420 m year^{-1} to keep up with this change. In comparison, the average velocity for temperature change since the last glacial maximum was only 5.9 m year^{-1} (Corlett & Westcott 2013). The migration capacity of plant species across the landscape depends on the species. Its range was placed at 1.7 to 1500 m year^{-1}, with most species dispersing less than a kilometre per year and many much less (Corlett & Westcott 2013). Only a minor number of typical calcareous grassland species have been found to be capable of long-distance dispersal by wind (Poschlod et al. 1998). Corlett & Westcott (2013) therefore concluded that many plant species will not be able to keep up with the velocity of climate change predicted for the next 100 years. These estimates from modelling studies emphasise the need for climate change adapted management, with a focus on securing migration corridors and refugia in an otherwise fragmented landscape (Streitberger et al. 2017). Creating habitat networks to connect isolated remnants of species-rich grasslands is becoming ever more important in the face of climate change (De Kort et al. 2018). This might often mean also protecting less valuable sites to create stepping stones and corridors (Pärtel et al. 2005). Deliberate dispersal of target species may also become a more important aspect of nature conservation in the future (Corlett & Westcott 2013). As we found in our resurvey study, the flat and north-facing slopes were less impacted by the drought. They may therefore serve as refugia for semi-arid calcareous grassland species in the future. However, they simultaneously showed a tendency towards eutrophication, with slightly increasing numbers of nutrient demanding species and mean Ellenberg indicator values for nutrients. Climate change adapted habitat management should aim to counteract these trends in order to increase the sites' suitability as refugia in the future.

6.2 Methodological limitations: Pseudo-turnover, baseline turnover, and others

Observational ecological data are often considered to be "noisy", containing a considerable amount of (apparently) random variation (Økland 1990; Palmer 1993; Zuur et al. 2010). To extract a "signal" from this noisy data, and to identify deterministic patterns and their drivers, is usually the aim of scientific studies. Noise is introduced into the data by environmental stochasticity, such as random dispersal events (e.g. by wind or animals), or animal behaviour (trampling, grazing) (Økland 1990), by errors in the data collection, and by chance in the assembly of species (termed "neutral stochasticity" by Vellend et al. (2014)). It remains a philosophical question whether there is such a thing as true chance (Vellend et al. 2014). The fundamental processes that drive species composition (birth, death, immigration, emigration) may ultimately be deterministic, but can appear random due to our incomplete understanding of complex ecological systems (Vellend et al. 2014). To conceptualise noise and signal in resurvey studies, we developed a framework that divides observed changes into three components: (i) the "signal" – the actual directional change, mostly driven by some external factor, (ii) methodologically induced pseudo-turnover, and (iii) stochastic fluctuations without directional change (introduced as "baseline turnover" in Mazalla et al. (2024)).

Dissimilarity indices are a widely used method for quantifying the difference in species composition between two vegetation samples. In the simplest case, a dissimilarity index can be understood as the percentage of species that are present in only one of the two plots being compared, relative to the total number of species observed (Jaccard index, Legendre & De Cáceres (2013)). Abundance-based versions additionally take into account the cover values of species, allowing for the consideration of more subtle shifts in abundance. Dissimilarity indices are able to summarise the complex, multivariate information on species identities into a single value. This enables comparisons among studies and the statistical analysis of differences in species composition. However, the interpretation of the value of such an index is not straightforward. Indices mostly have lower and upper limits whose meanings are clearly defined (with the exception of the Euclidean distance and similar indices, Legendre & De Cáceres (2013)). The lower limit of zero usually indicates that there is no difference in species composition, while the upper limit (most often 1, sometimes $\sqrt{2}$, Legendre & De Cáceres (2013)) indicates that there are no shared species between plots. However, it is unclear whether a value of, e.g. 0.38, such as the average pairwise dissimilarity in the *Nardus* grasslands, should be considered high or low, or, in the context of nature conservation, a cause for concern.

In order to confidently interpret the results of resurvey studies and to evaluate the extent to which the observed change can be attributed to noise rather than to deterministic vegetation change, it is vital to directly address the uncertainties that necessarily arise in every resurvey study. It may be useful to compare the observed dissimilarity in a resurvey study to estimates of methodological pseudo-turnover and baseline turnover. In the following sections, the two resurvey studies in this thesis are discussed with regard to different aspects of methodological uncertainty, such as pseudo-turnover, baseline turnover, study design, and the effect of "regression to the mean".

6.2.1 Methodological pseudo-turnover

The three aspects of methodological pseudo-turnover are relocation error, observer error, and seasonal error. All three result from partly inevitable inaccuracies that arise during fieldwork (for an introduction, see Section 1.5).

Relocation error

In the *Nardus* grasslands, relocation error can be assumed to have been reasonably small, as the original surveyor had put much effort into documenting the location of the plots accurately (precisely drawn maps at 1:5000 scale, Mazalla et al. (2021)). These maps were geo-referenced and the resulting coordinates were located in the field using a differential GPS to an accuracy of up to 2 cm. They were then marked in place by two magnets buried in the ground in diagonal corners, allowing for a future revisitation of the now permanently marked plots. The relatively large plot size (20 m^2) further reduced the impact of relocation error (Kopecký & Macek 2015). Compared to smaller plots, relocalisation needs to be less accurate in large plots to still match a large proportion of the original area (i.e. an error of 1 m would result in a total miss for a 1 m^2 plot, but only in missing approximately one fourth of the original area in a 4 × 5 m plot, Dodd (2011)).

In the calcareous grassland resurvey, relocation error was probably higher (Mazalla et al. 2022). It relied entirely on GPS data, which was recorded during the initial study and retrieved in the follow-up using a handheld device with typical inaccuracies of three to five metres. Additionally, the plot size was relatively small, measuring only 1 m^2. Therefore, the GPS inaccuracy exceeded the size of the squares, which is potentially problematic (Dodd 2011). However, the majority of resurvey studies that explicitly investigated the impact of relocation error on the reliability of their results have shown them to be robust to relocation error (Fischer & Stöcklin 1997; Ross et al. 2010; Kopecký & Macek 2015; Verheyen et al. 2018). An exception is the study by Boch et al. (2019) from Swiss dry grasslands which found that the turnover of species increased with GPS inaccuracy. Still, changes in ecological indicator values were robust to relocation error.

Observer error

In the *Nardus* grasslands, observer error may have been a relevant factor, especially concerning the identification of mosses. The original study had a focus on bryophytes (Ludwig 1987), which was not the case in the resurvey. Here, the two observers did also not meet in the field as recommended by Morrison (2016). Species identification was instead practised with another experienced botanist prior to the survey. In the calcareous grasslands, it was fortunately possible to carry out the first relevés of the resurvey together with one of the two original observers. In both studies, we took precautions by aggregating critical taxa, which has been shown to lower pseudo-turnover substantially (Boch et al. 2022). Studies of observer error have placed common values in grasslands at 10 % to 20 % (Lepš & Hadincová 1992; Kercher et al. 2003; Vittoz & Guisan 2007 in Morrison 2016). These seem likely for the *Nardus* grasslands but probably overestimate observer-induced pseudo-turnover in the calcareous grasslands. The reliability of cover value estimates is dependent on the plot size, with plots larger than 4 m^2 being difficult to oversee from a vertical point of view (Morrison 2016). The 1 m^2 plots in the calcareous grasslands therefore allowed for a more straightforward estimation of cover values. Accordingly, the analyses of the 20 m^2 plots in the *Nardus* grassland survey relied mostly on the frequency of species. In both studies, bryophytes were recorded additionally to the vascular plants. This led to an increased sampling time due to a second thorough searching of the plot after the vascular species had been noted. Often, one or several previously overlooked vascular species were discovered during this additional search. Generally, the completeness of species lists increases with sampling time in a curvilinear way, approaching an observer-specific maximum (Morrison 2016). We are therefore confident that the completeness of the vascular species list in both studies was high. Ideally, the time spent recording one plot should be similar between the initial and the follow-up survey. To avoid compromising the quality of the results by working too quickly, Archaux et al. (2006) recommended fixing the amount of time spent per plot, adjusted according to the expected species richness. This criterion was not taken into account while conducting the surveys. However, the average number of plots completed per day was very similar between surveys. In the *Nardus* grassland resurvey, an average of four plots were completed per day in the initial survey and three plots per day in the follow-up survey. In the calcareous grasslands, the numbers amounted to ten vs. eight plots, respectively. Assuming that a full working day was typically spent surveying plots, it can be expected that the thoroughness of the surveys was similar.

Seasonal error

Differences in the phenology between initial and follow-up survey may also have increased pseudo-turnover, especially in the estimated cover values. For the *Nardus* grasslands, the resurvey study was performed earlier in the year than the initial survey, and the summer of both survey years was exceptionally dry. The few existing geophytes were still present in the survey period in 2018 (end of May to beginning of July). In 1986, however, the author had to supplement the relevés carried out in August with notes from earlier inspections in the spring (Ludwig 1987). Apart from this, it is likely that the species list was not particularly influenced by the season, as most of the species present can be clearly distinguished also in the vegetative state. As a precaution, all analyses were carried out with presence/absence data and only complemented with results from abundance data where informative.

For the calcareous grasslands, the two investigation periods were more similar with just two weeks difference. However, calcareous grasslands host a number of spring ephemerals that may have been missed in the later summer surveys. Indeed, the number of annual species recorded decreased in the later relevés in the 2019 survey, which was conducted during an unusually dry summer.

6.2.2 Baseline turnover

We introduced “baseline turnover” as a measure of the amount of vegetation change that occurs regularly due to stochastic fluctuations in species composition, without any directional change between observations (Mazalla et al. 2024). While the role of methodological pseudo-turnover is widely acknowledged, the role of stochasticity in species composition for the observation of vegetation change has been largely neglected. Baseline turnover was calculated by regressing the dissimilarity in species composition between samples of the same plot – on the y-axis – to their temporal distance on the x-axis. The y-intercept of this model, i.e. the theoretical dissimilarity at zero temporal distance, was taken as a measure for baseline turnover (illustrated in Figure A5). This follows the reasoning that as the temporal distance is reduced to zero, no differences in conditions between plots should remain, leaving only the component of chance to explain differences in species composition (Brownstein et al. 2012). This is the first time baseline turnover was calculated from time series in a global context, following the development of the theory using a local spatial data set (Brownstein et al. 2012).

Baseline turnover was found to differ substantially between the vegetation types considered in the study, with forests expressing lower levels than semi-natural grasslands, and steppe/prairie and desert vegetation showing the highest amounts. The plot size on which the vegetation was recorded, the saturation of the plot with species from the community pool, the mean annual temperature, and the life form of occurring species each had a significant impact on baseline turnover. The baseline turnover levels observed were similar to commonly reported values of methodological pseudo-turnover. It is therefore a relevant factor to consider when attempting to disentangle signal from noise in observed vegetation change.

To extract plausible levels of baseline turnover for the two grasslands types featured in this thesis, we focus on baseline turnover values for semi-natural grasslands. We found the average baseline turnover for temperate grasslands in general to be 0.17 (Sørensen dissimilarity, based on presence/absence data, Table A15). More specifically, for two (semi-)arid calcareous grasslands, it amounted to an average of 0.12. However, the plots used to calculate this estimate had a size of 16 m^2 and were therefore much larger than the ones used in the resurvey study in calcareous grasslands (1 m^2, Mazalla et al. (2022)). The amount of baseline turnover was shown to increase in smaller plots. Across all vegetation types, this increase amounted to an average of 0.17 units of the Sørensen dissimilarity index per logarithmic step (for example going from 10 m^2 to 1 m^2). In a statistic approximation, 1 m^2 plots in calcareous grasslands might therefore have baseline turnover values of around 0.32 ($= 0.12 + 0.17 \cdot \log_{10}(16)$). We therefore conclude that stochastic fluctuations in species composition contributed to the observed turnover in the calcareous grasslands resurvey (mean 0.4 across all plots) to a high extent.

The vegetation of the resurveyed *Nardus* grasslands was approximately matched by three datasets in Mazalla et al. (2024), with baseline turnover values ranging from 0.03 to 0.08 (Table A15). In this case, the plot sizes in the resurvey study in the Eifel (20 m^2) were larger than those from which baseline turnover was estimated (0.25–4 m^2). The amount of turnover generated by non-directional fluctuations can therefore be expected to be even lower here than found in Mazalla et al. (2024), possibly in the range of 0.02 to 0.05. Accordingly, baseline turnover can be regarded as a potentially negligible factor in the *Nardus* grasslands, where the observed amount of vegetation change averaged 0.38. The difference between the two vegetation types can probably be explained by the fact that dry grasslands are more exposed to disturbances in the form of drought events and also, as a result, contain more annual species than *Nardus* grasslands, leading to a higher number of species regularly (dis)appearing by chance in a plot.

6.2.3 Regression to the mean

During the statistical analyses of resurvey study data, uncertainties in the interpretation arise from the inevitable noise in the data. Naturally, in a resurvey study, the variables of interest are measured at least twice, once in the initial and once in the follow-up survey. Due to unavoidable measurement errors, the observed values will always digress from a theoretical “true” or “exact” value. Measurement errors are typically assumed to follow a normal distribution, meaning that they have an equal probability of increasing or decreasing the observed value and that small errors occur more frequently than large ones. This means that if the observation-induced error in the initial measurement was large, it is likely that it will be smaller, i.e. move the observed value closer to the “true” value, in the follow-up measurement. In consequence, those values that were accidentally overestimated in the initial survey are likely to decrease in the follow-up survey (and vice versa), without any ecological reason. This effect is called “regression to the mean” and has first been described by Francis Galton in the 19th century (Stigler 1997). The phenomenon is well known in the medicinal literature but has rarely been considered in ecological research. In this thesis, its implications for resurveys and longitudinal experiments in vegetation ecology were presented (Mazalla & Diekmann 2022).

Regression to the mean may affect the interpretation of resurveys in which the samples in the initial study were not chosen randomly from the total sample (i.e. the sites), but selected, for example, for apparent species richness (Palmer 1993). To illustrate, imagine a grassland site across which a number of plots are placed randomly. The species numbers in those plots would be approximately normally distributed with the expected value of the distribution giving the average species number across the site. If the same number of plots were placed subjectively, for example selected for maximising apparent species richness as to cover the most “interesting” parts of the meadow, only an upper portion of the whole normal distribution of species richness would be selected for the initial survey. This upper portion would likely include patches where the “true” species number was overestimated by chance (i.e. had a large positive measurement error) at this initial time point. Those patches will exhibit lower species numbers in a follow-up measurement, simply due to regression to the mean. Even without any actual change in the average species number of the site, it might then appear to have decreased in the follow-up survey. This is one of the mechanisms by which the analysis of data from non-random samples can become risky (Lájer 2007).

Models that attempt to identify the drivers of the observed changes may also be affected by regression to the mean. Such a model is usually constructed in a way that the change score of a variable, i.e. the difference between the initial and the follow-up measurement, ($changescore = observation_{\text{follow-up}} - observation_{\text{initial}}$) is taken as the dependent variable. One or several environmental variables serve as predictors. The aim of such a model is to quantify the impact of the predictors on the change score. The effects of potential drivers may be estimated incorrectly if the predictor variable is correlated with the initial observation

(Mazalla & Diekmann 2022). We therefore recommended to include the initial values of the dependent variable (the $observation_{\text{initial}}$) into the model as a predictor as well, to correct for the effect of regression to the mean (EMA 2015; Mazalla & Diekmann 2022).

In Mazalla et al. (2022), we applied this approach. Here, the impact of microclimate (south- vs. north-facing slopes) on the change scores of eleven variables was examined in one model each. Including the $observation_{\text{initial}}$ as a predictor, as recommended, did not change the outcome of the models in seven of the eleven models. In these cases, the model estimate for microclimate influence retained the same sign and significance. In one case, the model became insignificant due to the correction, but the tendency that character species of dry grasslands had declined on south-facing slopes while they increased on north-facing slopes remained. In three cases, the sign of the model estimate changed from positive to negative due to the correction for regression to the mean. Ecologically, this altered the interpretation of the model results, even though the models remained insignificant in both versions. In the case of the Ellenberg indicator value for soil moisture, the uncorrected model predicted a weaker decrease in soil moisture in response to the drought on the drier south-facing slopes, while the model including a correction for regression to the mean predicted a stronger decrease. Mean Ellenberg indicator values for nutrients were also modelled to have increased on the south-facing slopes without correction, while they showed a decrease with the correction. Ecologically, both corrected versions are more intuitive to interpret, as it is more logical that soil moisture would be more strongly reduced on the warmer south-facing slopes. We have seen that accounting for the regression to the mean effect does not necessarily change model outcomes every time. If it does, it can however change the interpretation of model results in important ways.

"Spurious correlation" is another statistical issue that occurs when change scores are regressed against their corresponding initial values (Kenney 1982; Jackson & Somers 1991). It has to be distinguished from regression to the mean. Whereas regression to the mean stems from measurement errors, spurious correlations arise solely from statistical artefacts. In fact, the expected correlation of the change score ($= observation_{\text{follow-up}} - observation_{\text{initial}}$), regressed against its $observation_{\text{initial}}$, can be calculated with a formula derived from the definition of the correlation coefficient (Kenney 1982). If there is no correlation between the variables $observation_{\text{follow-up}}$ and $observation_{\text{initial}}$ and their standard deviations are equal, the correlation between the $changescore$ and its $observation_{\text{initial}}$ will by definition have a coefficient of -0.71, and therefore appear highly relevant (Kenney 1982). This is due to the fact that the $observation_{\text{initial}}$ is part of the $changescore$, therefore appearing on both sides of the correlation. Correlations such as these should be interpreted with great caution, both because of the effect of regression to the mean and because of spurious correlations. How to correctly disentangle the different statistical effects from each other and from the ecological interpretation is a matter of further research, although there are promising starting points in the field of medicine (Tu et al. 2005).

6.2.4 General methodological discussion

Study design

The use of non-randomly placed plots has been found to affect the analysis of resurvey studies (Palmer 1993; Lájer 2007, Section 1.5.2). In our resurvey study of *Nardus* grasslands, the original plot layout was based on subjective criteria. In order to avoid redundant data sampling, the initial study design did not consider widespread, almost pure *Molinia* stands according to their extent at the time (Ludwig 1987). In the calcareous grasslands, a stratified approach was chosen, in which the plots were also positioned subjectively within the strata. Both approaches attempted to represent the existing vegetation as completely as possible but at the same time failed to meet the requirement of random sampling for accurate statistical testing. The concerns raised in Section 1.5.2 about the appropriateness of statistical tests and the interpretation of changes in this biased sampling scheme therefore apply to both studies (Palmer 1993; Lájer 2007). One potential issue with this setup is the risk of overestimating the occurrence of rare species during the initial survey. Diekmann et al. (2007) found an increased number of rare species in subjectively placed plots compared to randomly placed plots. Indeed, in both the calcareous and *Nardus* grasslands, the rarest species in the initial studies (maximum five occurrences across all plots), showed a median decrease of one occurrence in the follow-up surveys. Due to the subjective study design, this trend may be a consequence of the regression to the mean effect.

Under-represented vegetation types in the initial study cannot be adequately captured with their floristic changes in a resurvey study. While species richness and evenness have increased in plots with a dominance of *Molinia* in the initial study of *Nardus* grasslands ($>$ 50 % cover, n = 22), more of this dynamic could have been detected if the *Molinia* stands had been sampled more extensively. Moreover, 33 ha of spruce plantations adjacent to the *Nardus* grasslands have been cut down as part of a EU-funded LIFE+ project between the surveys (BioStation 2018). These sites are now managed for grassland development and were initialised by the transfer of hay cuttings from *Nardus* grasslands. This expansion of valuable grassland area could not be recorded by the resurvey study either. In order to accurately monitor the development of vegetation types or landscapes, one cannot rely solely on comparisons with historical datasets, but must also consider what has happened outside the scope of these records.

Comparing observed dissimilarity to pseudo-turnover and baseline turnover

Morrison (2016) generally advised against interpreting turnover below 25 % as actual change, as this amount could regularly be entirely due to pseudo-turnover caused by observer error. More specifically, values of observer error in grasslands were reported to be in the range of 0.1–0.2 (Morrison 2016). While this estimate may be appropriate for the *Nardus* grassland resurvey, it is likely an overestimate for the calcareous grassland resurvey (see Section 6.2.1). Relocation error was probably negligible in the *Nardus* grasslands, while it may

Table 6.1: Subtracting estimates for methodological pseudo-turnover and baseline turnover from the amount of observed vegetation change (Sørensen dissimilarity presence/absence-based) in the two resurvey studies.

	Nardus grassland	Calcareous grassland	Reference
Observed change	0.38	0.40	
Baseline turnover	0.02–0.05	0.15–0.20	Mazalla et al. (2024)
Observer error	0.10–0.20	0.02–0.05	Morrison (2016)
Relocation error	0.02–0.05	0.10–0.30	spatial heterogeneity estimate
Difference	0.08–0.24	0.00–0.13	

have been a major factor in the calcareous grasslands. In the *Nardus* grasslands, the average species turnover between the initial and the resurvey study was 0.38 (Sørensen dissimilarity, presence/absence-based). Subtracting an estimate of 0.1–0.2 for observer error, a low estimate of 0.02–0.05 for relocation error, and 0.02–0.05 for baseline turnover (see Section 6.2.2) leaves an informed guess of 0.08–0.24 change (Table 6.1). In the calcareous grasslands, the average temporal turnover was 0.4. Here, observer error was probably well controlled. As it cannot be eliminated completely, we may place it at 0.02–0.05. Relocation error likely played an important role due to the GPS technology with a low accuracy and small plot sizes. A rough estimate for relocation error may be derived from the spatial heterogeneity of the sites. The average dissimilarity between plots in the same site in the follow-up survey was 0.39, with average distances between plots of 34 m. Plots with a distance of less than 10 m, which is a more realistic distance for relocation error using a GPS device, had average dissimilarities of 0.32. In extreme cases, relocation error might therefore reach 0.3. A lower bound is more difficult to define and may be set arbitrarily at 0.1. Baseline turnover can be assumed to be 0.15–0.2 based on the estimates in Section 6.2.2. Subtracting the estimates for pseudo-turnover and baseline turnover from the observed temporal turnover in calcareous grasslands leaves an amount of 0–0.13 of species turnover (Table 6.1).

These dissimilarity values describe the amount of vegetation change in a neutral way. However, they do not reflect whether the vegetation changes were directional, i.e. whether the replaced or added species share ecological properties or if the turnover simply represents a circling through the species pool (Baeten et al. 2014). In order to interpret the ecological meaning of the observed dissimilarities, detailed trends in single species or species groups have to be analysed. Testing for the significance of, e.g. changes in the abundance of a particular species group or in an ecological indicator, can indicate whether the observed turnover was directional. In both studies, we found several significant detailed trends, e.g. increases in small sedge sward species and soil pH in the *Nardus* grasslands, that indicate that distinct directional changes have occurred over the survey period. Another method to assess the significance of species turnover is the permutational multivariate analysis of variance (“Permanova”, Oksanen et al. 2019). For both resurvey studies, a Permanova indicated a significant difference in species composition between the surveys.

Statistical power of tests

It remains an open question whether the resurveys as a tool for conservation monitoring were, as Legg & Nagy (2006) put it, “a waste of time” or not. Studies with too few replications (i.e. plots) are susceptible to type II errors (accepting the null hypothesis, even though it is false), meaning actual differences might have been disregarded as non-significant and thus, according to the prevailing interpretation of significance, as non-existent (Legg & Nagy 2006). Calculating the power of statistical tests or the minimum detectable difference with the number of plots available and the expected amount of variation was beyond the scope of the studies. There is therefore a risk that existing trends may have been missed.

6.3 Conclusions and perspectives

This thesis provides new insights into the long-term development of *Nardus* grasslands and the response of calcareous grasslands to extreme drought periods. In the *Nardus* grasslands, regular mowing at a relatively early date proved to be a suitable method to counteract eutrophication induced by increased soil pH values and atmospheric deposition. It resulted in a characteristic structure and species composition. The same management was not suitable for the preservation of wet heaths. The resurvey study in calcareous grasslands showed a significant effect of the extreme summer droughts on their vegetation, increasing the share of dry grassland specialists and ruderal species. While in the past, the specialised vegetation has profited on sites with a warmer and drier microclimate, this may no longer be the case with ongoing climate change, as steep and south-facing slopes were affected more strongly by the drought, even resulting in a loss of character species. It can be challenging to generalise such findings, as results of resurvey studies are frequently specific to a particular site or habitat. In order to confidently identify common trends, additional resurvey studies should be conducted with suitable historical material. This may prove especially challenging for comparatively rare vegetation types like *Nardus* grasslands. To effectively protect grassland biodiversity, the insights of resurvey studies have to be communicated to nature conservation practitioners and local authorities. This was easily possible in the case of the *Nardus* grasslands, as they are all managed by a single “biological station”. In the case of the calcareous grasslands, this proved more difficult due to the fact that they are scattered over five municipalities.

Resurvey studies are a powerful tool to study long-term vegetation development. The associated methodological uncertainties presented in this thesis apply to all resurvey studies, even if they are carefully planned and conducted. We believe that the methodological concepts covered in this thesis have the potential to increase the accuracy of resurvey studies. The separation of signal from noise in the collected data has been a long-standing goal in vegetation ecology. To this end, the concept of baseline turnover can be employed to estimate the amount of stochastic fluctuations in species composition. To increase the confidence of baseline turnover estimates, they should be calculated for more datasets than it was possible in the scope of this thesis. The impact of study design on the statistical analyses of resurvey studies should be carefully considered to ensure a high quality and reliability of results. Resurvey studies are based on historical datasets, which have often been recorded without taking these criteria into account. Researchers should therefore select their source material carefully and be aware of the consequences of the data structure. This includes raising awareness of statistical issues such as regression to the mean, which may not always be popular because of their technical nature.

Grasslands are widespread semi-natural habitats with great potential for biodiversity and many more ecosystem services. Their functioning is endangered by multiple threats, most notably the effects of land use change. To effectively counteract biodiversity loss, it is crucial to have accurate information on grassland trends and their drivers. Another source of vulnerability is the ongoing climate change. Most information on the sensitivity of grassland types and their species currently comes from short-term experiments or modelling studies that predict the impact of future climate change. However, as the effects of climate change begin to be felt, resurvey studies offer further potential for a more direct assessment of the effects of climate change on grasslands.

6.4 References

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— Chapter 7 —

Appendices

Grazing of calcareous grasslands in the nature reserve “Gallberg” near Hildesheim, Lower Saxony, Germany.

7.1 Appendix: *Nardus* grasslands and wet heaths are affected differently by reintroduction of management and pH recovery

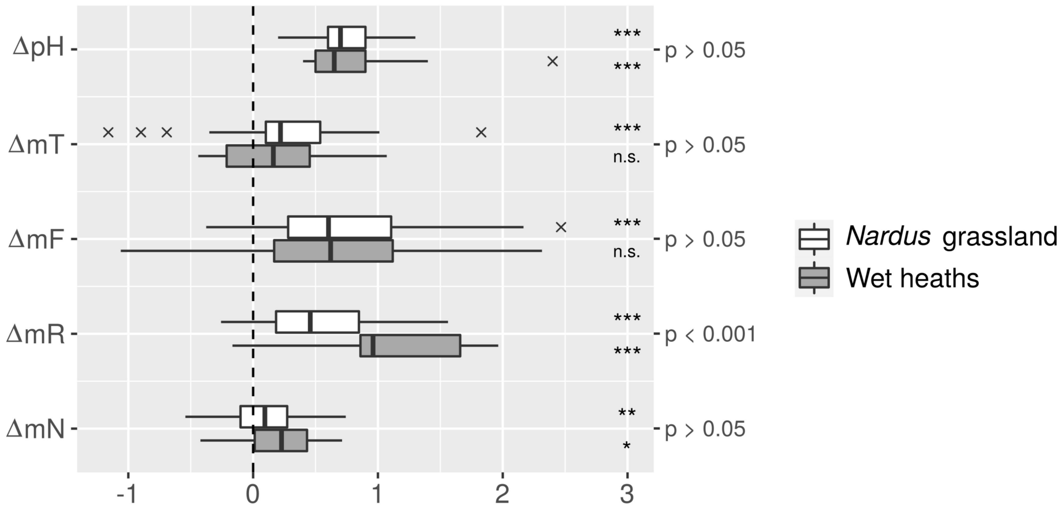

Figure A1: Changes of pH and cover-weighted Ellenberg indicator values for temperature (mT), soil moisture (mF), soil reaction (mR) and soil nutrients (mN).
Significance symbols (*** $p<0.001$ ** $p<0.01$ * $p<0.05$ n.s. $p>0.05$) indicate differences in indicator values between 1986 and 2018. Out-written p values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.
Abbildung A1: Veränderungen von pH-Wert und mit Deckungsgraden gewichteten Ellenberg-Zahlen für Temperatur (mT), Bodenfeuchte (mF), Bodenreaktion (mR) und Nährstoffe (mN).
Sternchen (*** $p<0{,}001$ ** $p<0{,}01$ * $p<0{,}05$ n.s. $p>0{,}05$) geben das Signifikanz-Niveau von Unterschieden der Zeigerwerte zwischen 1986 und 2018 an. Ausgeschriebene p-Werte geben die Signifikanz von Unterschieden zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.

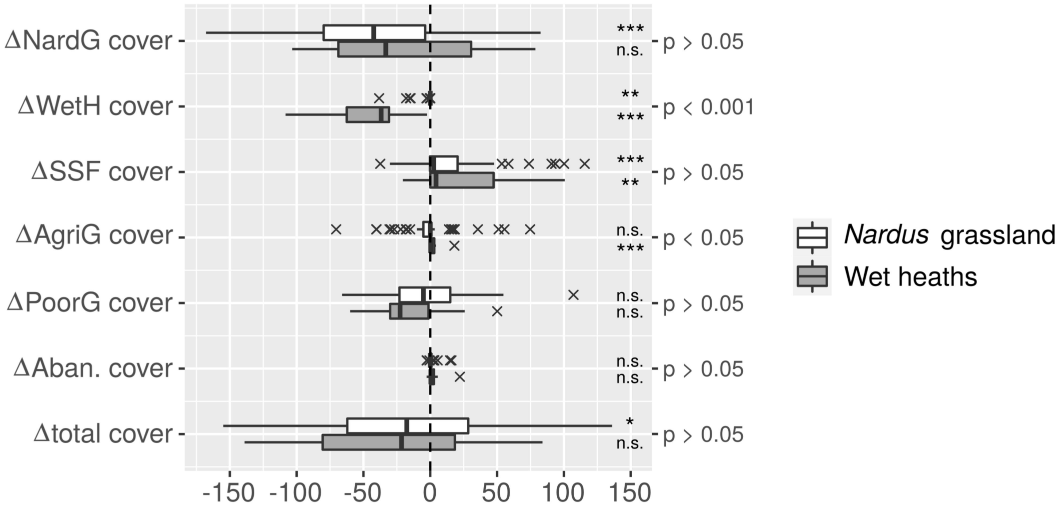

Figure A2: Changes in total cover and cover sums of character species groups. NardG = character species of *Nardus* grasslands; WetH = character species of wet heaths; SSF = character species of small sedge fens; AgriG = species of agricultural grasslands; PoorG = other species of nutrient-poor grasslands; Aban = fallow indicators. Significance symbols (*** $p<0.001$ ** $p<0.01$ * $p<0.05$ n.s. $p>0.05$) indicate differences in species group cover between 1986 and 2018. Out-written p values give the significance of differences between *Nardus* grasslands and wet heaths. Tests: Wilcoxon signed rank test.

Abbildung A2: Veränderungen von Gesamtdeckung und Deckungssummen von Artengruppen. NardG = Charakterarten der Borstgrasrasen; WetH = Charakterarten der Feuchtheiden; SSF = Charakterarten der Kleinseggenriede; AgriG = Arten des Wirtschaftsgrünlands; PoorG = andere Arten mageren Grünlands; Aban = Brachezeiger. Sternchen (*** $p<0{,}001$ ** $p<0{,}01$ * $p<0{,}05$ n.s. $p>0{,}05$) geben das Signifikanz-Niveau von Unterschieden der Deckungssummen der Artengruppen zwischen 1986 und 2018 an. Ausgeschriebene *p*-Werte geben die Signifikanz von Unterschieden zwischen Borstgrasrasen und Feuchtheiden an. Tests: Wilcoxon-Vorzeichen-Rang-Tests.

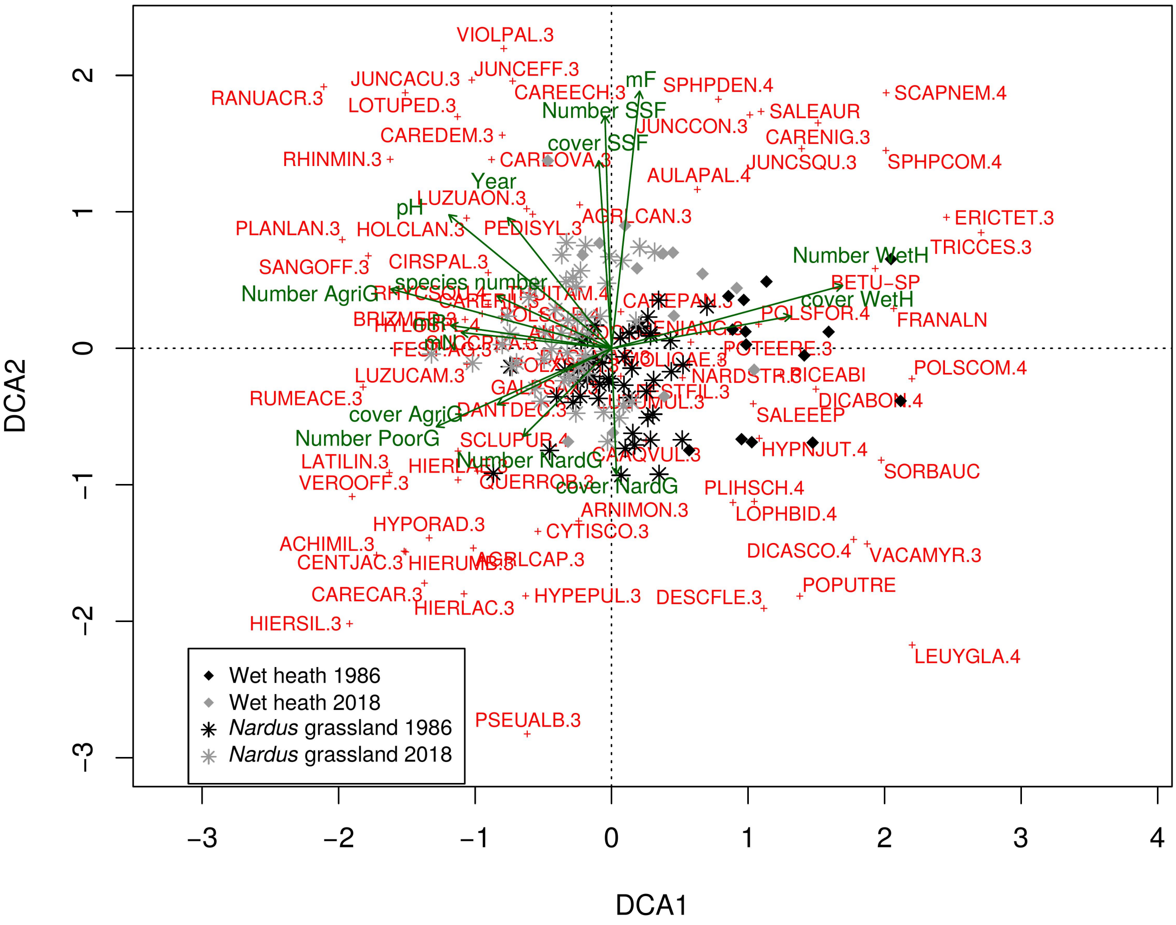

Figure A3: DCA of all plots in 1986 and 2018 based on species presence/absence data, only species with at least 10 occurrences in the total dataset are displayed. Environmental variables included are significantly correlated to one of the two first DCA axis ($p < 0.05$) with $R^2 \geq 0.15$. mF, mR and mN: presence/absence based Ellenberg indicator values for soil moisture, soil reaction and soil nutrients; Species numbers (Number) and cover sums (cover) of the following species groups: NardG = character species of *Nardus* grasslands, WetH = wet heath character species, SSF = species of small sedge fens, AgriG = agricultural grassland species, and PoorG = species of other poor grasslands; Axis length is 3.45 for axis 1 and 2.31 for axis 2.

Abbildung A3: DCA aller Aufnahmen von 1986 und 2018, basierend auf Präsenz/Absenz-Daten. Nur Arten mit mindestens 10 Vorkommen im Gesamtdatensatz sind dargestellt. Dargestellte Umweltvariablen sind signifikant mit einer der beiden DCA-Achsen korreliert ($p < 0.05$), mit $R^2 \geq 0.15$. mF, mR und mN: Präsenz/Absenz-basierte Ellenberg-Zahlen für Bodenfeuchte, Bodenreaktion und Nährstoffe; Artenzahl (Number) und Deckungssummen (cover) der Artengruppen: NardG = Charakterarten der Borstgrasrasen, WetH = Charakterarten der Feuchtheiden, SSF = Charakterarten der Kleinseggenriede, AgriG = Arten des Wirtschaftsgrünlands, PoorG = Arten anderer nährstoffarmer Wiesen. Achsenlänge ist 3.45 für Achse 1 und 2.31 für Achse 2.

Table A1: Mean and standard deviations of pH values and presence/absence-based Ellenberg indicator values for soil reaction (mR) and nutrients (mN) for *Nardus* grasslands and wet heaths in 1986 and 2018. Small letters indicate significant differences between the groups. Groups were tested for similarity with a pairwise Wilcoxon rank sum test corrected for multiple comparisons with the “Bonferroni”-method.

Tabelle A1: Mittelwerte und Standardabweichungen von pH-Werten und Präsenz/Absenz-basierten Ellenberg-Zahlen für Bodenreaktion (mR) und Nährstoffe (mN) in Borstgrasrasen und Feuchtheiden in 1986 und 2018. Hochgestellte Buchstaben geben die Signifikanz von Unterschieden zwischen den Gruppen an. Tests auf signifikante Unterschiede wurden mit einem paarweisen Wilcoxon-Vorzeichen-Rang-Test durchgeführt und mit der „Bonferroni"-Methode für multiple Vergleiche korrigiert.

	***Nardus* grasslands**		**Wet heaths**	
	1986	2018	1986	2018
pH	3.94 (0.20)^{a}	4.67 (0.23)^{b}	3.62 (0.33)^{c}	4.44 (0.37)^{d}
mR	3.10 (0.30)^{a}	3.40 (0.25)^{a}	2.36 (0.18)^{b}	3.14 (0.49)^{a}
mN	2.49 (0.19)^{a}	2.55 (0.20)^{a}	2.29 (0.35)^{b}	2.56 (0.37)^{ab}

Table A2: Changes of single species in *Nardus* grasslands in frequency and cover value between 1986 and 2018. Habitat and taxonomic group abbreviations: see Table A8. T, F, R, N: Ellenberg indicator values for temperature, soil moisture, soil reaction and nutrients. p-value: Wilcoxon signed rank test of differences, adjusted for false detection rate (“fdr”).
Levels of significance: *** $p < 0.001$ ** $p < 0.01$ * $p < 0.05$.
Tabelle A2: Veränderungen einzelner Arten in Borstgrasrasen hinsichtlich Frequenz und Abundanz zwischen 1986 und 2018. Abkürzungen der taxonomischen und Habitat-Gruppen: siehe Tab. A8. T, F, R, N: Ellenberg-Zahlen für Temperatur, Bodenfeuchte, Bodenreaktion und Nährstoffe. p-Werte: Wilcoxon-Vorzeichen-Rang-Tests, korrigiert für die Falscherkennungsrate („fdr”).
Signifikanz-Niveaus: *** $p < 0{,}001$ ** $p < 0{,}01$ * $p < 0{,}05$.

	freq 1986	freq 2018	Δfreq	Δ cover	habitat group	taxon. group	T	F	R	N
Increase Frequency & Cover										
Carex pilulifera	17	47	30**	5.19***	SSF	Gram	.	5	3	3
Pedicularis sylvatica	20	45	25***	1.42*	NardG	Dico	5	8	1	2
Carex echinata	0	22	22***	2.57***	SSF	Gram	.	8	3	2
Rhinanthus minor	1	20	19***	0.08***	AgriG	Dico	5	4	.	3
Quercus robur	0	13	13*	0.02*	Aban	Phan	6	.	.	.
Increase Frequency										
Plantago lanceolata	3	17	14*	0.40	AgriG	Dico	.	.	.	.
Increase Cover										
Rhytidiadelphus squarrosus	39	48	9	15.34*	Indiff.	Moss	3	6	5	.
Danthonia decumbens	39	48	9	11.49***	NardG	Gram	.	.	3	2
Hylocomium splendens	27	42	15	5.38*	Indiff.	Moss	.	.	.	.
Juncus acutiflorus	1	14	13	0.99*	PoorG	Gram	6	8	5	3
							Ø 5.0	6.5	3.3	2.5
Decrease Frequency & Cover										
Lophocolea bidentata	30	0	−30***	−0.45***	WetH	Moss	3	6	5	.
Pleurozium schreberi	50	27	−23***	−18.24***	Indiff.	Moss	3	4	2	.
Luzula multiflora	32	13	−19*	−0.21*	NardG	Gram	.	5	5	3
Dicranum scoparium	27	9	−18**	−0.53***	NardG	Moss	.	4	4	.
Hypnum jutlandicum	48	27	−11***	−5.12**	Indiff.	Moss	3	2	2	.
Decrease Frequency										
Aulacomnium palustre	39	22	−17**	−1.94	Indiff.	Moss	2	7	3	.
Decrease Cover										
Nardus stricta	47	48	1	−20.25***	NardG	Gram	.	.	2	2
Festuca filiformis	50	48	−2	−6.23***	NardG	Gram	6	4	3	2
Arnica montana	37	26	−11	−4.43**	NardG	Dico	4	5	3	2
Polytrichum commune var. *perigionale*	33	22	−11	−3.56**	Indiff.	Moss	.	.	.	.
Polygala serpyllifolia	43	44	1	−0.48***	NardG	Dico	4	6	2	2
							Ø 3.6	4.8	3.1	2.2
							$p =$ 0.11	$p =$ 0.09	$p =$ 0.65	$p =$ 0.55

Table A3: Changes of single species in wet heaths in frequency and cover value between 1986 and 2018. Habitat and taxonomic group abbreviations: see Table A8. T, F, R, N: Ellenberg indicator values for temperature, soil moisture, soil reaction and nutrients. p-value: Wilcoxon signed rank test of differences, adjusted for false detection rate. Levels of significance: *** $p< 0.001$ ** $p< 0.01$ * $p< 0.05$.

Tabelle A3: Veränderungen einzelner Arten in Feuchtheiden hinsichtlich Frequenz und Abundanz zwischen 1986 und 2018. Abkürzungen der taxonomischen Gruppen und Habitat-Gruppen: siehe Tab. A8. T, F, R, N: Ellenberg-Zahlen für Temperatur, Bodenfeuchte, Bodenreaktion und Nährstoffe. p-Werte: Wilcoxon-Vorzeichen-Rang-Tests, korrigiert für die Falscherkennungsrate („fdr”). Signifikanz-Niveaus: *** $p< 0{,}001$ ** $p< 0{,}01$ * $p< 0{,}05$.

	freq 1986	**freq 2018**	**Δfreq**	**Δcover**	**habitat group**	**taxon. group**	**T**	**F**	**R**	**N**
Increase Frequency & Cover										
Rhytidiadelphus squarrosus	0	13	13^{***}	15.21^{**}	Indiff.	Moss	3	6	5	.
Increase Cover										
Agrostis canina	2	11	9	3.83^{*}	SSF	Gram	5	9	3	2
Decrease Cover										
Erica tetralix	12	6	6	-13.50^{*}	Indiff	dw. shrub	5	8	1	2

Table A4: Coefficients for best multiple linear regression models for changes in Ellenberg indicator values for soil reaction (mR) and nutrients (mN), presence/absence-based (p/a) and abundance-weighted (cov) respectively. pH 1986, Fallow index 1986, mF 1986: pH, fallow-index and Ellenberg indicator value for soil moisture as measured in 1986. ΔpH, ΔmF: changes in pH and Ellenberg indicator value for soil moisture between 1986 and 2018. WH: factor variable for syntaxon, sites with wet heath in 1986 as opposed to *Nardus* grassland. WH:mF1986, WH:ΔmF, WH:pH1986: interaction terms with wet heath. p-values were calculated with a type III test (t-test). Share: share of explained variance calculated with hierarchical partitioning.
Tabelle A4: Koeffizienten der besten linearen Modelle für Veränderungen von Ellenberg-Zeigerwerten für Bodenreaktion (mR) und Nährstoffe (mN), sowohl Präsenz/Absenz-basiert (p/a) als auch mit Deckungsgrad gewichtet (cov). pH 1986, Fallow index 1986, mF 1986: pH, Brache-Index und Ellenberg-Zahlen für Bodenfeuchte in 1986. ΔpH, ΔmF: Veränderungen des pH-Werts und der Ellenberg-Zahl für Bodenfeuchte zwischen 1986 und 2018. WH: Faktor-Variable für Syntaxon, Aufnahmen mit Feuchtheide in 1986 im Gegensatz zu Borstgrasrasen. WH:mF1986, WH:ΔmF, WH:pH1986: Interaktionsterme der jeweiligen Variablen mit dem Faktor „Feuchtheide". *p*-Werte wurden mit einem Typ-III Test (t-test) berechnet. Share: Anteil erklärter Varianz, berechnet mit hierarchischer Partitionierung.

	p	R^2	pH 1986	p/ share	ΔpH	p/ share	Fallow index 1986	WH	p/ share	Site	p/ share	mF 1986	p/ share	ΔmF	p/ share	WH: mF 1986	p/ share	WH: ΔmF	p/ share	WH: pH 1986	p/ share
ΔmR p/a	<0.001	0.38	.	.	.	.	.	0.67	<0.001 100%	.	.	.	.	.	.	.	.	.	.	.	.
ΔmR cov	<0.001	0.24	−0.32	0.353/ 3%	.	.	.	−6.29	0.006/ 40%	.	.	−0.27	0.033/ 10%	.	.	.	.	.	.	1.85	0.003/ 47%
ΔmN p/a	<0.001	0.44	.	.	.	.	.	−2.22	0.070/ 6%	9 coeff.	<0.001/ 80%	−0.03	0.773/ 1%	−0.03	0.697/ 1%	0.42	0.043/ 7%	−0.37	0.038/ 6%	.	.
ΔmN cov	<0.001	0.08	.	.	0.25	0.017/ 100%	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table A5: Coefficients for best multiple linear regression models for changes in species numbers and Sørensen indices, calculated with presence/absence data (qualitative) or cover values (quantitative) respectively. pH 1986, Fallow index 1986: pH, fallow index as measured in 1986. ΔpH: changes in pH between 1986 and 2018. WH: factor variable for syntaxon, sites with wet heath in 1986 as opposed to *Nardus* grassland. p-values were calculated with a type III test (t-test). Share: share of explained variance calculated with hierarchical partitioning.
Tabelle A5: Koeffizienten der besten multiplen linearen Modelle für Veränderungen von Artenzahlen und Sørensen-Indizes, berechnet mit Präsenz/Absenz-Daten (qualitativ) und Deckungsgraden (quantitativ). pH 1986, Fallow index 1986: pH und Bracheindex in 1986. ΔpH: Veränderungen des pH-Werts zwischen 1986 und 2018. WH: Faktor-Variable für Syntaxon, Aufnahmen mit Feuchtheide in 1986 im Gegensatz zu Borstgrasrasen. p-Werte wurden mit einem Typ-III Test (t-test) berechnet. Share: Anteil erklärter Varianz, berechnet mit hierarchischer Partitionierung.

	p	R^2	pH 1986	p/ share	ΔpH	p/ share	Fallow index 1986	p/ share	WH	p/ share	Site	p/ share
Δspecies number total	<0.001	0.28	.	.	.	.	.	.	11.31	<0.001/ 100 %	.	.
Δspecies number vascular	<0.001	0.27	.	.	5.13	0.041/ 23 %	.	.	8.19	<0.001/ 77 %	.	.
Δspecies number bryophytes	<0.001	0.19	.	.	.	.	−1.70	0.021/ 26 %	18.83	<0.001/ 74 %	.	.
Sørensen quantitative	n.s.	.	.	.	.	.	.	.	.	.	.	.
Sørensen qualitative	<0.001	0.41	0.17	0.020/ 8 %	0.11	0.034/ 7 %	0.01	0.002/ 24 %	0.20	<0.001/ 62 %	.	.

Table A6: Coefficients for best multiple linear regression models for changes in species group presence (p/a) and cover sums (cover) respectively. Species groups: NardG = character species of *Nardus* grasslands; SSF = character species of small sedge fens; AgriG = species of agricultural grasslands; PoorG = other species of nutrient-poor grasslands. pH 1986, Fallow index 1986: pH and fallow index as measured in 1986. ΔpH: changes in pH between 2018 and 1986. WH: factor variable for syntaxon, sites with wet heath in 1986 as opposed to *Nardus* grassland. *p*-values were calculated with a type III test (t-test). Share: share of explained variance calculated with hierarchical partitioning.
Tabelle A6: Koeffizienten der besten multiplen linearen Modelle für Veränderungen der Artengruppen Frequenz (p/a) und Deckungssummen (cover). Artengruppen: NardG = Charakterarten der Borstgrasrasen; SSF = Charakterarten der Kleinseggenriede; AgriG = Arten des Wirtschaftsgrünlands; PoorG = andere Arten mageren Grünlands. pH 1986, Fallow index 1986: pH und Bracheindex in 1986. ΔpH: Veränderungen des pH-Werts zwischen 1986 und 2018. WH: Faktor-Variable für Syntaxon, Aufnahmen mit Feuchtheide in 1986 im Gegensatz zu Borstgrasrasen. *p*-Werte wurden mit einem Typ-III Test (t-test) berechnet. Share: Anteil erklärter Varianz, berechnet mit hierarchischer Partitionierung.

	p	R^2	pH 1986	p/ share	ΔpH	p/ share	Fallow index 1986	p/ share	WH	p/ share	Site	p/ share	WH: pH 1986	p/ share
ΔNardG p/a	n.s.	.	.	.	.	.	.	.	.	.	.	.	.	.
ΔNardG cover	<0.001	0.47	.	.	−46.04	0.015/ 5 %	7.76	0.007/ 14 %	−67.64	0.033/ 7 %	9 coeff.	<0.001/ 75 %	.	.
ΔAgriG p/a	0.006	0.13	.	.	2.58	0.030/ 51 %	.	.	1.97	0.035/ 49 %	.	.	.	.
ΔAgriG cover	n.s.	.	.	.	.	.	.	.	.	.	.	.	.	.
ΔSSF p/a	0.003	0.15	.	.	16.55	0.014 55 %	.	.	11.74	0.027 45 %	.	.	.	.
ΔSSF cover	n.s.	.	.	.	.	.	.	.	.	.	.	.	.	.
ΔPoorG p/a	0.001	0.19	−3.54	0.018/ 23 %	.	.	.	.	−20.24	0.018/ 36 %	.	.	5.81	0.011/ 41 %
ΔPoorG cover	n.s.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table A7: Results of an RDA on species differences between 1986 and 2018, based on presence/absence (p/a) and square-root transformed cover values (cover) respectively. Predictor variables were automatically selected via permutation testing. ΔpH: changes in pH between 2018 and 1986. Wet heath: factor variable for syntaxon, sites with wet heath in 1986 as opposed to *Nardus* grassland. Share: share of explained variance calculated by anova.
Tabelle A7: Ergebnisse einer RDA mit Differenzen aller Arten zwischen 1986 und 2018, basierend auf Präsenz/Absenz-Daten (p/a) bzw. Quadratwurzel-transformierten Deckungswerten (cover). Prädiktorvariablen wurden automatisch durch Permutationstests ausgewählt. ΔpH: Änderungen des pH-Werts zwischen 2018 und 1986. Wet heath: Faktor-Variable für Syntaxon, Aufnahmen mit Feuchtheide in 1986 im Gegensatz zu Borstgrasrasen. Share: Anteil der erklärten Varianz, berechnet durch eine anova.

	p	proportion constrained	ΔpH		ΔmF		Fallow index 1986		Wet heath		Site	
			p	share	*p*	share	*p*	share	*p*	share	*p*	share
species differences p/a	0.001	29%	0.001	3%	0.001	5%	.	.	.	.	0.001	22%
species differences cover	0.001	42%	.	.	0.001	8%	0.001	7%	0.001	5%	0.001	22%

Table A8: Complete list of species with habitat preference group and taxonomic group assignment. Taxonomic groups: Dico = herbaceous dicotyledones, Gram = graminoids, Phan = bushes and trees, dw. shrub = dwarf shrubs, Mono = herbaceous monocotyledones, Moss = cryptogams.
Habitat-preference groups: NardG = character species of *Nardus* grasslands from the class *Calluno-Ulicetea* Br.-Bl. et Tüxen 1943 ex Klika et Hadac 1944 (according to Peppler-Lisbach & Petersen 2001); WetH = character species of wet heaths from the class *Oxycocco-Sphagnetea* Br.-Bl. & Tx. Ex Westhoff et al. 1946 (group 1.8 in Ellenberg et al. 1992, classification of mosses according to Dierssen 1982); SSF: character species of small sedge fens (*Scheuchzerio-Caricetea nigrae* Tx. 1937, group 1.7 in Ellenberg et al. 1992, classification of mosses according to Dierssen 1982); AgriG = species of agricultural grasslands (*Molinio-Arrhenatheretea* Tx. 1937, group 5.4 in Ellenberg et al. 1992 with N > 3); PoorG = species of nutrient-poor grasslands (groups 5.2 – 5.4 in Ellenberg et al. 1992 with N <= 3); Aban: fallow indicators like trees, bushes and typical understorey species (groups 6 – 8 in Ellenberg et al. 1992). Red List Code (Metzing et al. 2018): V = early warning, 3 = endangered, 2 = highly endangered, / = not assessed, D = not enough data.

Tabelle A8: Vollständige Artenliste mit Zuordnung zu taxonomischen Gruppen und Habitat-Präferenz Gruppen. Taxonomische Gruppen: Dico = krautige Dikotyle, Gram = Grasartige, Phan = Bäume und Sträucher, dw. shrub = Zwergsträucher, Mono = krautige Monokotyle, Moss = Kryptogamen.
Gruppen der Habitatpräferenz: NardG = Charakterarten der Borstgrasrasen aus der Klasse *Calluno-Ulicetea* Br.-Bl. et Tüxen 1943 ex Klika et Hadac 1944 (nach Peppler-Lisbach & Petersen 2001); WetH = Charakterarten der Feuchtheiden aus der Klasse *Oxycocco-Sphagnetea* Br.-Bl. & Tx. Ex Westhoff et al. 1946 (Gruppe 1.8 in Ellenberg et al. 1992, Klassifikation der Moose nach Dierssen 1982); SSF = Charakterarten der Kleinseggenriede (*Scheuchzerio-Caricetea nigrae* Tx. 1937, Gruppe 1.7 in Ellenberg et al. 1992, Klassifikation der Moose nach Dierssen 1982); AgriG = Arten des Wirtschaftsgrünlands (*Molinio-Arrhenatheretea* Tx. 1937, Gruppe 5.4 in Ellenberg et al. 1992 mit N > 3); PoorG = weitere Arten des mageren Grünlandes (Gruppen 5.2 – 5.4 in Ellenberg et al. 1992 mit N <= 3); Aban = Brachezeiger wie Bäume, Büsche und typische Unterholz-Arten (Gruppen 6 – 8 in Ellenberg et al. 1992). Code der Roten Liste (Metzing et al. 2018): V = Vorwarnliste, 3 = gefährdet, 2 = stark gefährdet, / = nicht bewertet, D = nicht genug Daten.

	Red List BRD	**taxon. group**	**habitat group**
Achillea millefolium	.	Dico	AgriG
Achillea ptarmica	.	Dico	PoorG
Agrostis canina	.	Gram	SSF
Agrostis capillaris	.	Gram	AgriG
Anemone nemorosa	.	Dico	Indiff.
Angelica sylvestris	.	Dico	AgriG
Anthoxanthum odoratum	.	Gram	Indiff.
Anthyllis vulneraria	.	Dico	PoorG

	Red List BRD	**taxon. group**	**habitat group**
Arnica montana	3	Dico	NardG
Arrhenatherum elatius	.	Gram	AgriG
Athyrium filix-femina	.	Moss	Indiff.
Atrichum undulatum	.	Moss	Indiff.
Aulacomnium palustre	V	Moss	Indiff.
Barbilophozia kunzeana	2	Moss	Indiff.
Betonica officinalis	V	Dico	AgriG
Betula pendula	.	Phan	Aban
Betula pubescens	.	Phan	Aban
Botrychium lunaria	3	Moss	NardG
Brachythecium rivulare	.	Moss	Indiff.
Brachythecium rutabulum	.	Moss	Indiff.
Briza media	.	Gram	PoorG
Bryum caespiticium	.	Moss	Indiff.
Bryum pseudotriquetrum	.	Moss	SSF
Calluna vulgaris	.	dw. shrub	NardG
Calliergon stramineum	V	Moss	SSF
Calliergonella cuspidata	.	Moss	Indiff.
Calypogeia arguta	.	Moss	Indiff.
Calypogeia muelleriana	.	Moss	Indiff.
Calypogeia fissa	.	Moss	Indiff.
Caltha palustris	V	Dico	AgriG
Campylopus flexuosus	.	Moss	WetH
Campylopus fragilis	V	Moss	Indiff.
Campylopus introflexus	/	Moss	Indiff.
Campylopus pyriformis	.	Moss	Indiff.
Campanula rotundifolia	.	Dico	PoorG
Cardamine pratensis	.	Dico	Indiff.
Carex caryophyllea	V	Gram	PoorG
Carex demissa	V	Gram	SSF
Carex echinata	.	Gram	SSF
Carex flacca	.	Gram	Indiff.
Carex montana	.	Gram	Indiff.
Carex nigra	.	Gram	SSF
Carex ovalis	.	Gram	NardG
Carex pallescens	.	Gram	NardG
Carex panicea	V	Gram	SSF
Carex pulicaris	2	Gram	SSF
Carex remota	.	Gram	Aban
Carex pilulifera	.	Gram	NardG
Centaurea jacea agg.	.	Dico	PoorG

	Red List BRD	**taxon. group**	**habitat group**
Centaurea nigra subsp. *nemoralis*	.	Dico	PoorG
Cephalozia bicuspidata	.	Moss	Indiff.
Cerastium holosteoides	.	Dico	AgriG
Ceratodon purpureus	.	Moss	Indiff.
Cetraria islandica	2	Moss	Indiff.
Chamaespartium sagittale	V	Dico	NardG
Cirsium palustre	.	Dico	AgriG
Cladonia portentosa	3	Moss	Indiff.
Cladonia arbuscula subsp. *mitis*	3	Moss	Indiff.
Climacium dendroides	.	Moss	Indiff.
Colchicum autumnale	.	Mono	AgriG
Crataegus monogyna	.	Phan	Aban
Cytisus scoparius	.	Phan	Aban
Dactylorhiza maculata agg.	V	Mono	Indiff.
Dactylis glomerata	.	Gram	Indiff.
Danthonia decumbens	V	Gram	NardG
Deschampsia cespitosa	.	Gram	Indiff.
Deschampsia flexuosa	.	Gram	NardG
Dicranum bonjeanii	3	Moss	Indiff.
Dicranum polysetum	V	Moss	Indiff.
Dicranum scoparium	.	Moss	Indiff.
Dicranoweisia cirrata	.	Moss	Indiff.
Dicranella heteromalla	.	Moss	Indiff.
Diplophyllum albicans	.	Moss	Indiff.
Dryopteris carthusiana	.	Mono	Aban
Epilobium angustifolium	.	Dico	Aban
Epilobium montanum	.	Dico	Aban
Equisetum arvense	.	Moss	Indiff.
Erica tetralix	V	dw. shrub	WetH
Eriophorum angustifolium	V	Gram	SSF
Euphrasia frigida	2	Dico	NardG
Eurhynchium praelongum	.	Moss	Indiff.
Eurhynchium striatum	.	Moss	Indiff.
Fagus sylvatica	.	Phan	Aban
Festuca rubra agg.	.	Gram	AgriG
Festuca filiformis	.	Gram	NardG
Frangula alnus	.	Phan	Aban
Galium mollugo agg.	.	Dico	Indiff.
Galium palustre	.	Dico	Indiff.
Galium saxatile	.	Dico	NardG
Galium verum	.	Dico	PoorG

	Red List BRD	**taxon. group**	**habitat group**
Galium uliginosum	.	Dico	PoorG
Galeopsis tetrahit	.	Dico	Aban
Genista anglica	3	dw. shrub	NardG
Genista pilosa	V	dw. shrub	NardG
Gentiana pneumonanthe	2	Dico	PoorG
Gymnocolea inflata	V	Moss	Indiff.
Hedera helix	.	Phan	Aban
Helictotrichon pratense	V	Gram	PoorG
Heracleum sphondylium	.	Dico	AgriG
Hieracium lachenalii	.	Dico	NardG
Hieracium laevigatum	.	Dico	PoorG
Hieracium laurinum	.	Dico	Aban
Hieracium sabaudum	.	Dico	Aban
Hieracium pilosella	.	Dico	PoorG
Hieracium umbellatum	.	Dico	Aban
Holcus lanatus	.	Gram	AgriG
Holcus mollis	.	Gram	Aban
Hylocomium splendens	.	Moss	Indiff.
Hypericum maculatum	.	Dico	PoorG
Hypericum pulchrum	.	Dico	PoorG
Hypericum perforatum	.	Dico	Aban
Hypnum jutlandicum	.	Moss	NardG
Hypochaeris radicata	.	Dico	PoorG
Juncus acutiflorus	.	Gram	PoorG
Juncus articulatus	.	Gram	SSF
Juncus bufonius	.	Gram	Indiff.
Juncus bulbosus	.	Gram	Indiff.
Juncus conglomeratus	.	Gram	PoorG
Juncus effusus	.	Gram	AgriG
Juncus conglomeratus × *effusus*	.	Gram	AgriG
Juncus squarrosus	V	Gram	NardG
Jungermannia gracillima	V	Moss	Indiff.
Knautia arvensis	.	Dico	AgriG
Koeleria pyramidata	V	Gram	PoorG
Lathyrus linifolius	V	Dico	NardG
Lathyrus pratensis	.	Dico	AgriG
Leontodon autumnalis	.	Dico	AgriG
Leucanthemum ircutianum	.	Dico	AgriG
Leucobryum glaucum	.	Moss	Indiff.
Linum catharticum	.	Dico	PoorG
Lonicera periclymenum	.	Phan	Aban

	Red List BRD	**taxon. group**	**habitat group**
Lophocolea bidentata	.	Moss	Indiff.
Lophocolea heterophylla	.	Moss	Indiff.
Lophozia ventricosa	D	Moss	Indiff.
Lophozia wenzelii	.	Moss	Indiff.
Lotus corniculatus	.	Dico	PoorG
Lotus pedunculatus	.	Dico	AgriG
Luzula congesta	3	Gram	NardG
Luzula campestris	.	Gram	NardG
Luzula multiflora	.	Gram	NardG
Maianthemum bifolium	.	Mono	Aban
Melampyrum pratense	.	Dico	Aban
Mentha aquatica	.	Dico	Indiff.
Meum athamanticum	V	Dico	PoorG
Mnium hornum	.	Moss	Indiff.
Molinia caerulea	.	Gram	PoorG
Myosotis nemorosa	.	Dico	AgriG
Narcissus pseudonarcissus	3	Mono	NardG
Nardus stricta	V	Gram	NardG
Narthecium ossifragum	3	Mono	WetH
Odontoschisma sphagni	3	Moss	WetH
Pedicularis sylvatica	3	Dico	NardG
Phyteuma nigrum	V	Dico	AgriG
Picea abies	.	Phan	Aban
Pimpinella saxifraga	.	Dico	PoorG
Pinus sylvestris	.	Phan	Aban
Plantago lanceolata	.	Dico	AgriG
Platanthera bifolia	3	Mono	Indiff.
Platanthera chlorantha	3	Mono	Indiff.
Pleuridium acuminatum	.	Moss	Indiff.
Pleurozium schreberi	.	Moss	NardG
Plagiomnium rostratum	.	Moss	Indiff.
Plagiothecium laetum var. *curvifolium*	.	Moss	Indiff.
Poa humilis	.	Gram	PoorG
Poa trivialis	.	Gram	AgriG
Poa pratensis	.	Gram	AgriG
Pohlia nutans	.	Moss	Indiff.
Polytrichum commune var. *commune*	.	Moss	Indiff.
Polytrichum commune var. *perigoniale*	V	Moss	Indiff.
Polytrichum commune	.	Moss	Indiff.
Polytrichum formosum	.	Moss	Indiff.
Polygala serpyllifolia	3	Dico	NardG

	Red List BRD	**taxon. group**	**habitat group**
Polygala vulgaris	V	Dico	NardG
Populus tremula	.	Phan	Aban
Potentilla erecta	.	Dico	NardG
Primula veris	V	Dico	PoorG
Prunus avium	.	Phan	Aban
Prunus padus	.	Phan	Aban
Prunella vulgaris	.	Dico	AgriG
Pseudorchis albida	3	Mono	NardG
Pseudotaxiphyllum elegans	.	Moss	Indiff.
Ptilidium ciliare	3	Moss	NardG
Quercus petraea	.	Phan	Aban
Quercus robur	.	Phan	Aban
Ranunculus acris	.	Dico	AgriG
Ranunculus flammula	.	Dico	SSF
Ranunculus nemorosus	V	Dico	Indiff.
Ranunculus repens	.	Dico	AgriG
Rhizomnium punctatum	.	Moss	Indiff.
Rhinanthus minor	.	Dico	AgriG
Rhytidiadelphus squarrosus	.	Moss	Indiff.
Rubus fruticosus agg.	.	Phan	Aban
Rubus idaeus	.	Phan	Aban
Rumex acetosa	.	Dico	AgriG
Salix aurita	.	Phan	Aban
Salix caprea	.	Phan	Aban
Salix repens	.	Dico	PoorG
Salix × *multinervis*	.	Phan	Aban
Salix cinerea	.	Phan	Aban
Sanguisorba minor	.	Dico	AgriG
Sanguisorba officinalis	V	Moss	Indiff.
Scapania paludicola	2	Moss	Indiff.
Scapania nemorea	.	Moss	Indiff.
Scapania undulata	.	Moss	Indiff.
Scapania irrigua	V	Moss	Indiff.
Scleropodium purum	.	Dico	PoorG
Scorzonera humilis	3	Dico	AgriG
Silene flos-cuculi	.	Dico	Indiff.
Solidago virgaurea	.	Phan	Aban
Sorbus aucuparia	.	Phan	Aban
Sphagnum capillifolium	.	Moss	Indiff.
Sphagnum compactum	3	Moss	WetH
Sphagnum denticulatum var. *inundatum*	3	Moss	SSF

	Red List BRD	**taxon. group**	**habitat group**
Sphagnum denticulatum	.	Moss	SSF
Sphagnum fallax	.	Moss	SSF
Sphagnum magellanicum	3	Moss	WetH
Sphagnum molle	2	Moss	WetH
Sphagnum subsecundum	3	Moss	SSF
Sphagnum palustre	.	Moss	SSF
Sphagnum papillosum	3	Moss	WetH
Sphagnum quinquefarium	.	Moss	Indiff.
Sphagnum rubellum var. *subtile*	3	Moss	WetH
Sphagnum tenellum	2	Moss	WetH
Stellaria alsine	.	Dico	Indiff.
Stellaria graminea	.	Dico	Indiff.
Succisa pratensis	V	Dico	PoorG
Taraxacum sect. *Alpina et Hamata et Ruderalia*	.	Dico	AgriG
Teucrium scorodonia	.	Dico	Aban
Thesium pyrenaicum	3	Dico	PoorG
Thuidium delicatulum	V	Moss	Indiff.
Thuidium tamariscinum	.	Moss	Indiff.
Thymus pulegioides	.	Dico	PoorG
Trichophorum cespitosum subsp. *germanicum*	2	Gram	WetH
Trientalis europaea	.	Dico	Aban
Trifolium medium	.	Dico	Indiff.
Trifolium pratense	.	Dico	AgriG
Trifolium repens	.	Dico	AgriG
Vaccinium myrtillus	.	dw. shrub	NardG
Valeriana dioica	.	Dico	AgriG
Veronica chamaedrys	.	Dico	Indiff.
Veronica officinalis	.	Dico	NardG
Viburnum opulus	.	Phan	Aban
Vicia cracca	.	Dico	AgriG
Viola canina	V	Dico	NardG
Viola palustris	.	Dico	SSF
Viola reichenbachiana	.	Dico	Aban

7.2 Appendix: Microclimate shapes vegetation response to drought in calcareous grasslands

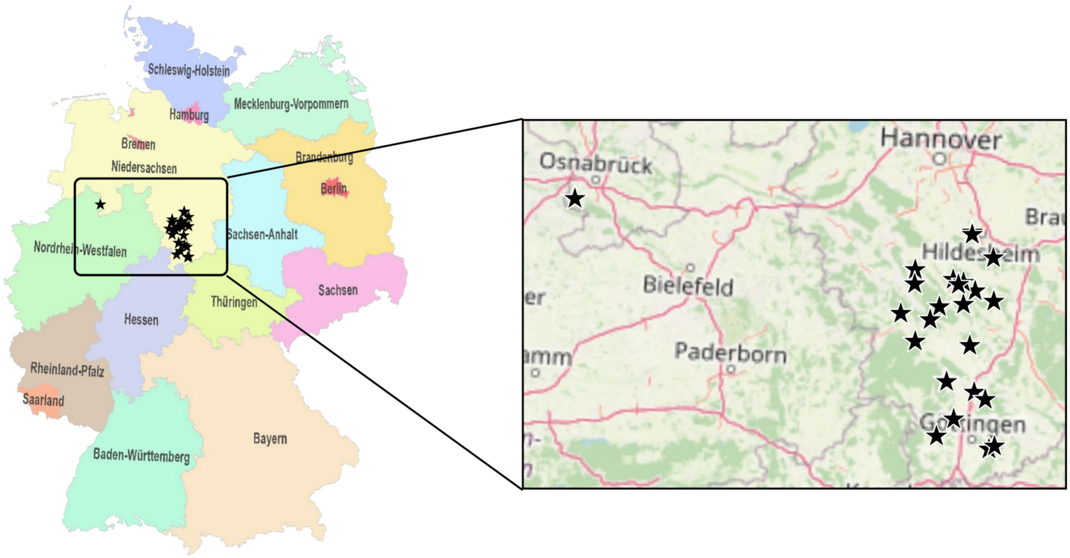

Figure A4: Map of the 25 study sites in North-West Germany. Background map sources: https://gdz.bkg.bund.de; osm.de

Table A9: Summary of mixed linear models for vegetation variables in 2008. Red and green marking indicates significant positive or negative influence of the predictor variable (columns) on the response variable (rows). mL, mF, mN: mean Ellenherg indicator values for light, soil moisture, and nutrients. P: soil phosphorus content. C/N: soil carbon to nitrogen ratio. G: grazed, GM: grazed and mown. % site variation: share of variance explained by the site as the random factor.

	R^2	heat index	incli- nation	P	soil depth	field capacity	C/N	land- use	heat index: soil depth	inclination: soil depth	soil depth: field capacity	heat index: C/N	% site variation
total richness	n.s.	.	.	.	.	.	.	.	.	.	.	.	56%
dry grasslands character species													
% species	0.26	0.28	.	-0.10	.	.	.	.	-0.02	.	.	.	48%
% cover	0.31	0.26	.	-0.02	.	.	0.004	.	.	.	.	.	66%
agricultural grassland species													
% species	0.37	-0.20	-0.002	0.02	.	.	.	.	.	.	.	0.008	13%
% cover	0.39	-107.32	-2.41	4.01	.	.	-1.34	.	.	0.13	.	3.67	32%
other poor grassland species													
% species	0.30	.	0.002	-0.01	0.007	0.001	.	G: 0.03, GM: -0.03	.	.	-0.00007	.	19%
% cover	n.s.	.	.	.	.	.	.	.	.	.	.	.	39%
ruderal species													
% species	n.s.	.	.	.	.	.	.	.	.	.	.	.	44%
% cover	n.s.	.	.	.	.	.	.	.	.	.	.	.	36%
mL	0.14	.	0.01	.	.	.	.	.	.	-0.0007	.	.	56%
mF	0.30	-122.68	.	4.26	.	.	.	.	.	.	.	3.53	67%
mN	0.50	-1.33	-0.03	0.07	-0.05	-0.007	.	.	.	0.002	0.0005	0.05	44%
grasses:forbs	n.s.	.	.	.	.	.	.	.	.	.	.	.	60%
evenness	0.10	.	-1.09	.	.	.	.	.	.	.	.	.	35%

7.3 Appendix: Regression to the mean in vegetation science

Table A10: Model coefficients of the linear model regressing the change in species number plot between 2002 and 2020 with soil potassium (K) content.

	Estimate	***p* value**	**Adjusted R^2**
Intercept	0.78	0.66	
log(Potassium)	1.52	0.05	0.02

Table A11: Model coefficients of the linear model regressing the change in species number per plot between 2002 and 2020 with soil potassium (K) content and species number in 2002 as a second predictor variable.

	Estimate	***p* value**	**Adjusted R^2**
Intercept	12.91	<0.001	
Species number 2002	-0.4	<0.001	
log(Potassium)	1.29	0.05	0.3

Table A12: Sources of the four exemplary datasets from resurvey studies.

Name	Vegetation Type	Location	Survey Years	Number of plots	Plot Size	Publication	Authors/ Owners
Nardus grassland	Violenion caninae, Juncenion squarrosi, Galium-saxatile-Nardus-stricta community (Peppler-Lisbach & Petersen 2001)	Eifel mountains, Germany	1986, 2018	50	20 m^2	Mazalla, L., Ludwig, G. & Peppler-Lisbach, C. (2021) '*Nardus* grasslands and wet heaths are affected differently by reintroduction of management and pH recovery'. *Tuexenia* 41, 227–252. DOI: https://doi.org/ 10.14471/2021.41.010	Gerhard Ludwig, Leonie Mazalla
Mesophilic to calcareous grasslands Werratal	From mown or grazed mesic grasslands (Arrhenatheretalia Tx. 1931) to mesic chalk grasslands (Bromion erecti Koch 1926)	Surroundings of Witzenhausen, Northern Hesse, Germany	2002, 2020	194	25 m^2	unpublished	Alexander Zilz, Mathis Oesterlen, Leonie Mazalla
Wet grasslands	Wet variants of intensively/extensively used agricultural grassland (species poor/rich Cynosurion, Arrhenatherion),Calthion (Tx. 1937) meadows, periodically wettened meadows (Potentillion anserinae Tx. 1947) and sedge reeds (Magnocaricion elatae Koch 1926)	Surroundings of Bremen, North-Western Germany	2010, 2016	60	2500 m^2	Gesamtbericht: Statistische Multivariate Auswertungen der IAG-Probegebietsdaten zum Grünland (2004–2016) in Bremen (Projekt Nr. 125)	Cecilia Dupré, Martin Diekmann
Chalk grasslands	Mesic chalk grasslands (Bromion erecti Koch 1926)	Southern Lower Saxony, Germany	2008, 2019	113	1 m^2	Mazalla, L., Diekmann, M., & Dupré, C. (2022) 'Microclimate shapes vegetation response to drought in calcareous grasslands'. *Applied Vegetation Science* 25(3), e12672. DOI:https://doi.org/ 10.1111/avsc.12672	Cecilia Duprè, Martin Diekmann, Leonie Mazalla

7.4 Appendix: Baseline turnover: accounting for stochasticity in studies of vegetation change

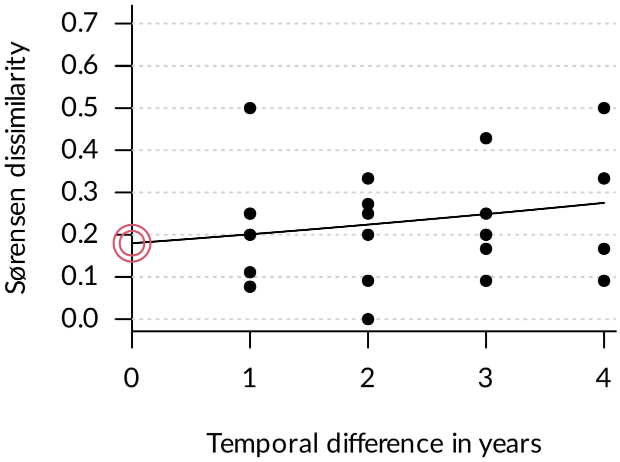

Figure A5: Illustration of the calculation of baseline turnover. y-axis: Sørensen dissimilarity values of one single plot (Dataset “aelmoeseneiebos”, Plot ID “1”, 0.25 m^2 in temperate deciduous forest), x-axis: temporal distance of the samples. A logistic model was fitted to the data. The intercept of this model (circled in red) represents the theoretical amount of dissimilarity at a temporal distance of zero (the “nugget”), which equals baseline turnover in our concept.

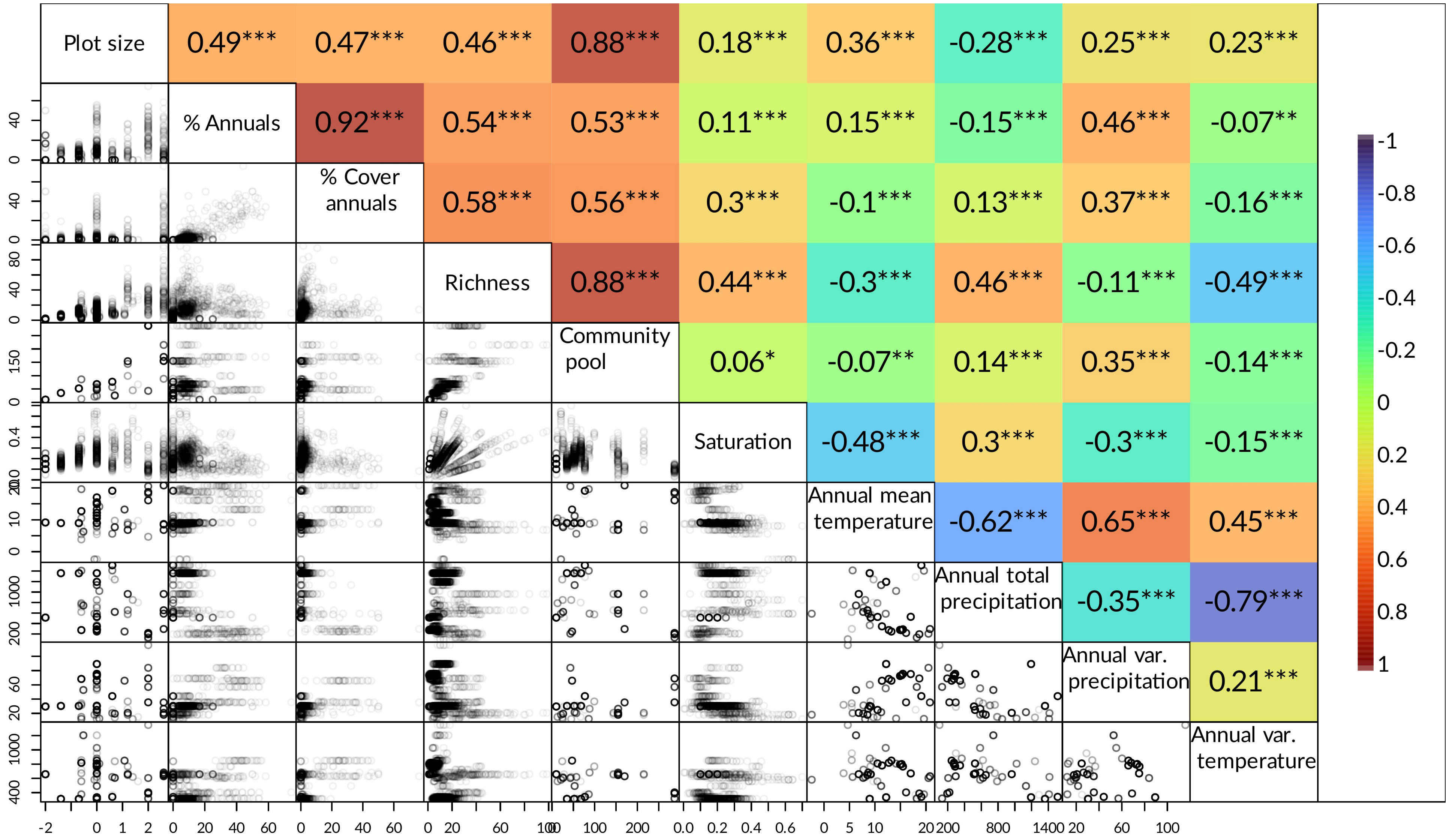

Figure A6: Scatterplots and correlation coefficients of a Spearman rank correlation between all predictor variables. Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; . $p < 0.01$.

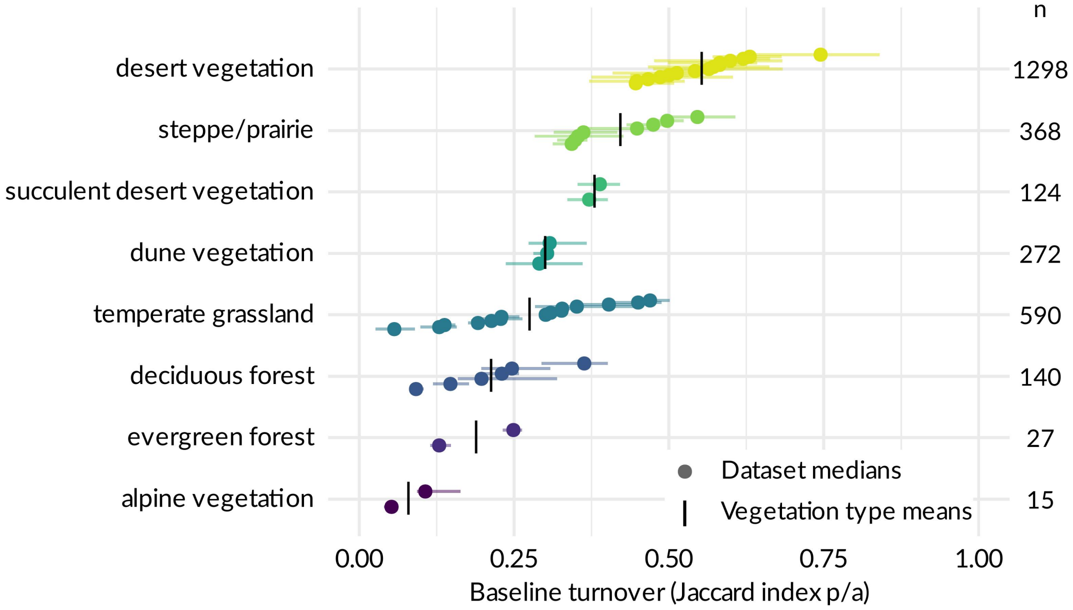

Figure A8: Levels of baseline turnover in eight different vegetation types. Baseline turnover is expressed using the **Jaccard dissimilarity index based on presence/absence data**; medians and 25 %–75 % quantile ranges are displayed per dataset, together with vegetation type means. Plots smaller than 0.25 m^2 and the vegetation type "mire" (with only one dataset) are omitted from this data summary. See Figure 5.4, A7, A9–A13 for corresponding results for the remaining seven dissimilarity indices.

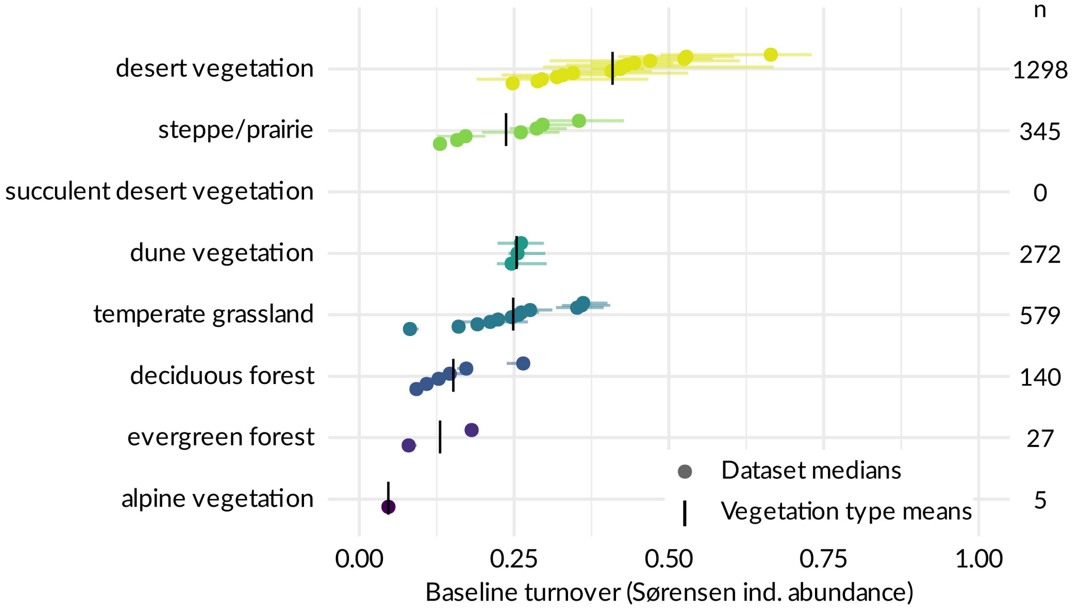

Figure A7: Levels of baseline turnover in eight different vegetation types. Baseline turnover is expressed using the **Sørensen dissimilarity index based on abundance data**; medians and 25 %–75 % quantile ranges are displayed per dataset, together with vegetation type means. Plots smaller than 0.25 m^2 and the vegetation type "mire" (with only one dataset) are omitted from this data summary. See Figure 5.4, A8–A13 for corresponding results for the remaining seven dissimilarity indices.

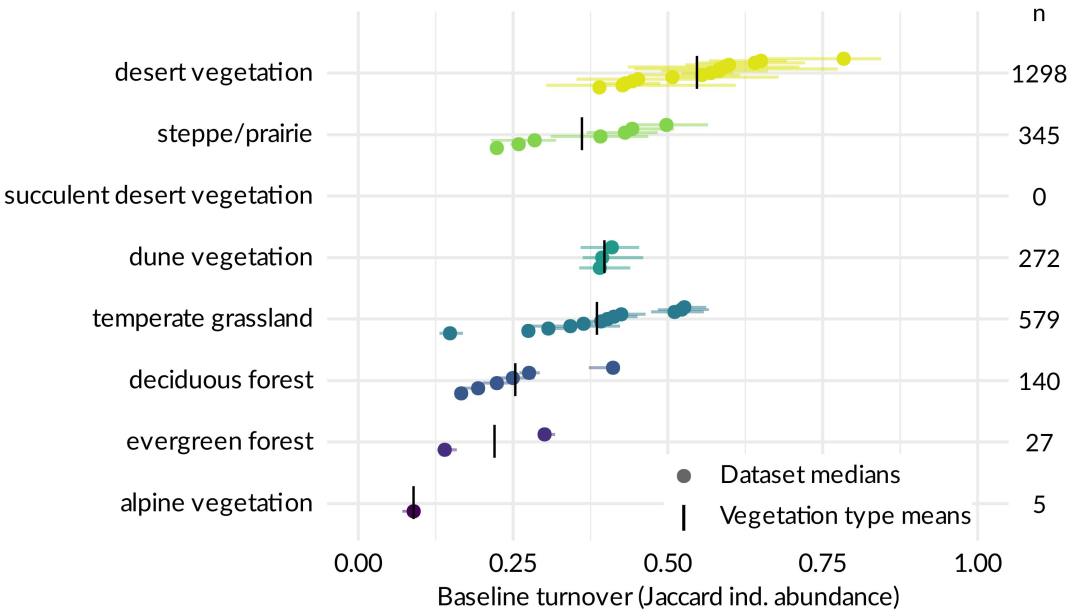

Figure A9: Levels of baseline turnover in eight different vegetation types. Baseline turnover is expressed using the **Jaccard dissimilarity index based on abundance data**; medians and 25 %–75 % quantile ranges are displayed per dataset, together with vegetation type means. Plots smaller than 0.25 m^2 and the vegetation type "mire" (with only one dataset) are omitted from this data summary. See Figure 5.4, A7–A8, A10–A13 for corresponding results for the remaining seven dissimilarity indices.

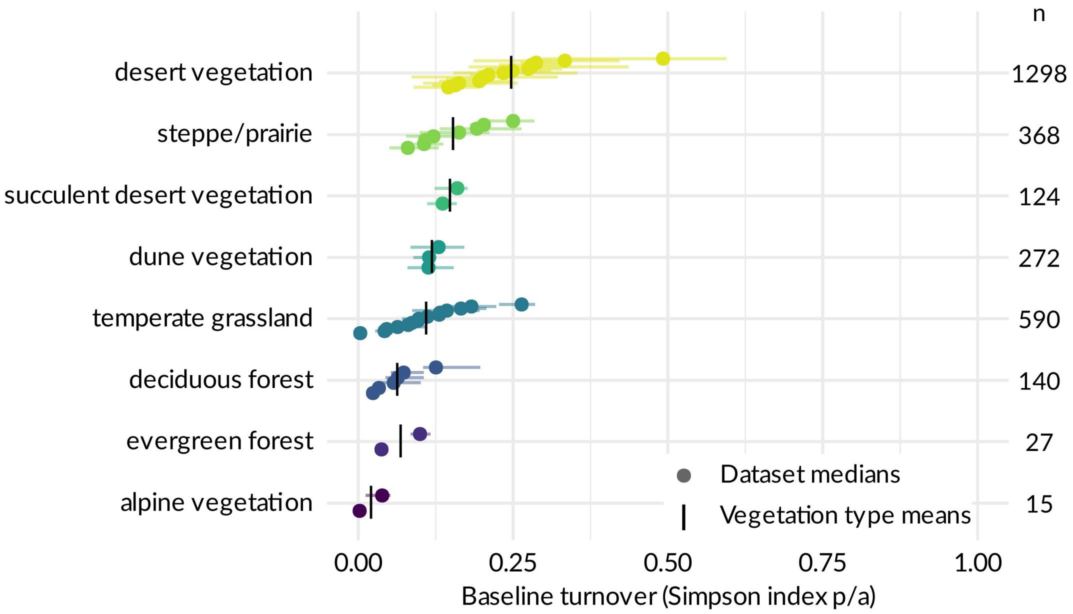

Figure A10: Levels of baseline turnover in eight different vegetation types. Baseline turnover is expressed using the **Simpson dissimilarity index based on presence/absence data**; medians and 25 %–75 % quantile ranges are displayed per dataset, together with vegetation type means. Plots smaller than 0.25 m^2 and the vegetation type "mire" (with only one dataset) are omitted from this data summary. See Figure 5.4, A7–A9, A11–A13 for corresponding results for the remaining seven dissimilarity indices.

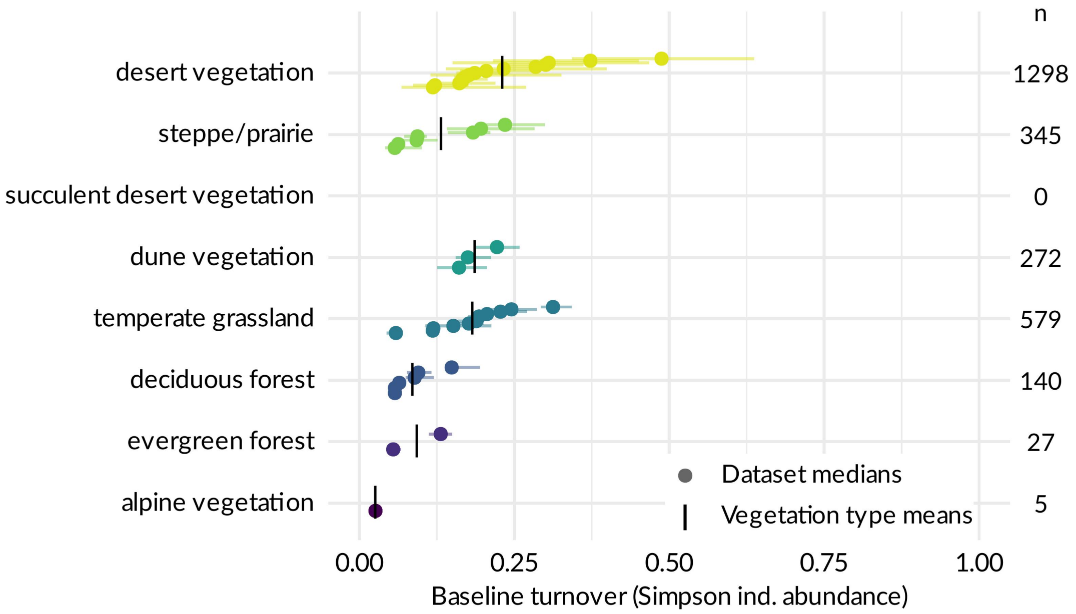

Figure A11: Levels of baseline turnover in eight different vegetation types. Baseline turnover is expressed using the **Simpson dissimilarity index based on abundance data**; medians and 25 %–75 % quantile ranges are displayed per dataset, together with vegetation type means. Plots smaller than 0.25 m^2 and the vegetation type “mire” (with only one dataset) are omitted from this data summary. See Figure 5.4, A7–A10, A12–A13 for corresponding results for the remaining seven dissimilarity indices.

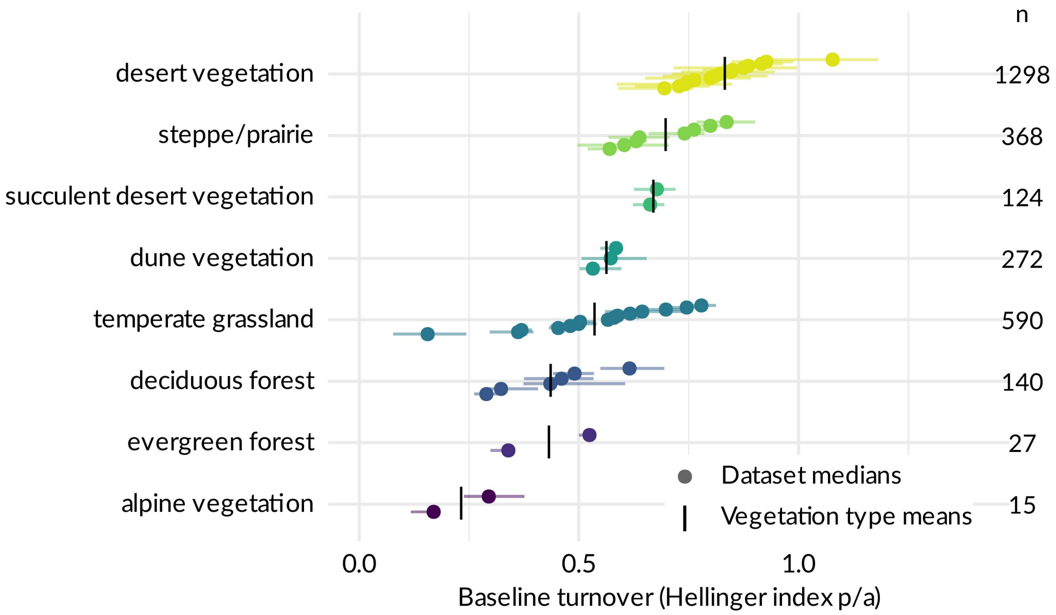

Figure A12: Levels of baseline turnover in eight different vegetation types. Baseline turnover is expressed using the **Hellinger dissimilarity index based on presence/absence data**; medians and 25 %–75 % quantile ranges are displayed per dataset, together with vegetation type means. Plots smaller than 0.25 m^2 and the vegetation type “mire” (with only one dataset) are omitted from this data summary. See Figure 5.4, A7–A11, A13 for corresponding results for the remaining seven dissimilarity indices.

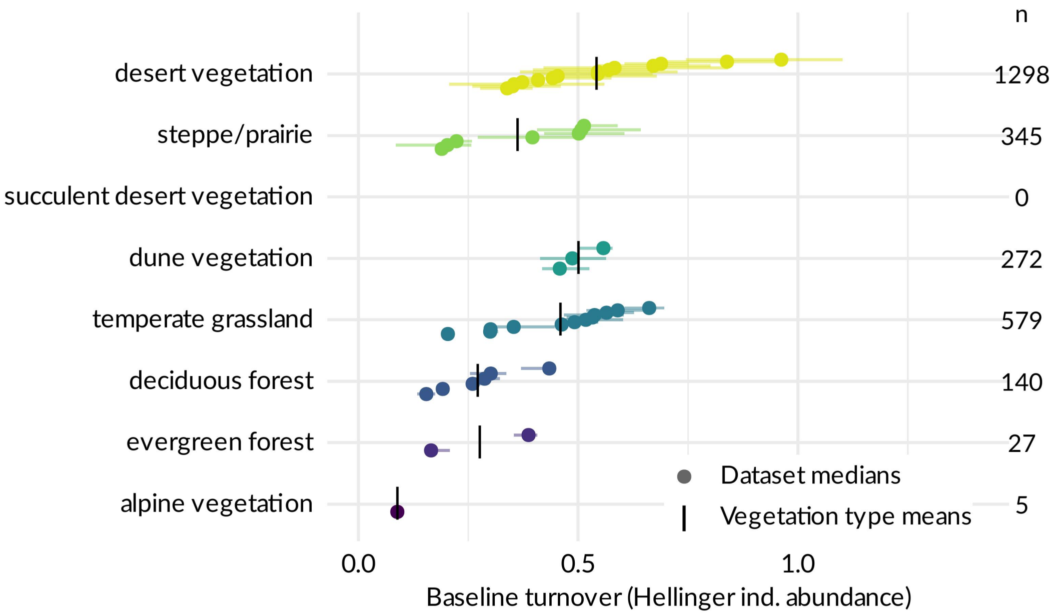

Figure A13: Levels of baseline turnover in eight different vegetation types. Baseline turnover is expressed using the **Hellinger dissimilarity index based on abundance data**; medians and 25 %–75 % quantile ranges are displayed per dataset, together with vegetation type means. Plots smaller than 0.25 m^2 and the vegetation type “mire” (with only one dataset) are omitted from this data summary. See Figure 5.4, A7–A12 for corresponding results for the remaining seven dissimilarity indices.

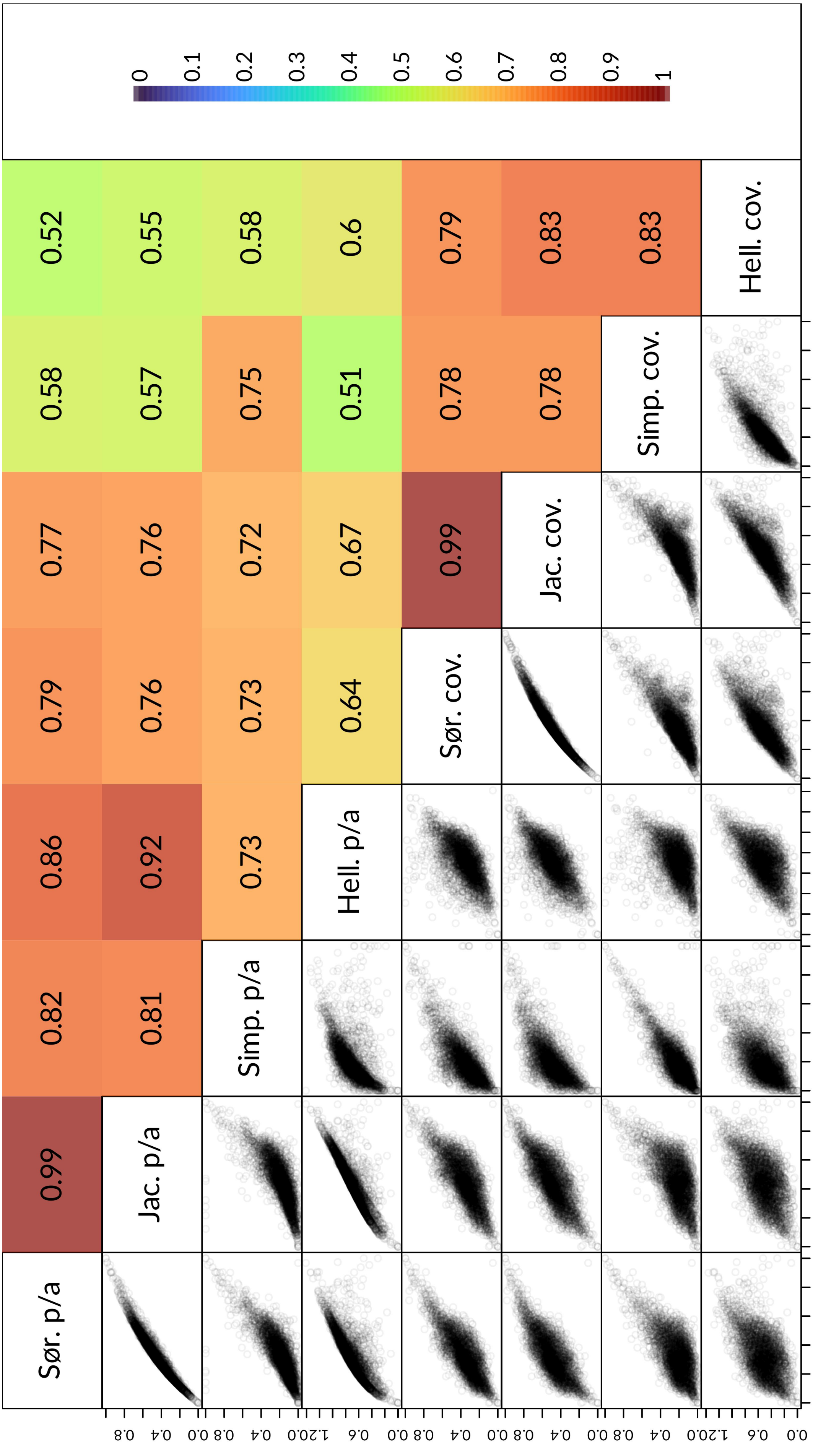

Figure A14: Scatterplots and correlation coefficients of a Spearman rank correlation between baseline turnover values based on the eight used dissimilarity indices (Sørensen, Jaccard, Simpson, Hellinger), each calculated with presence/absence (p/a) data and cover (cov.) data. All pairings had p values < 0.001.

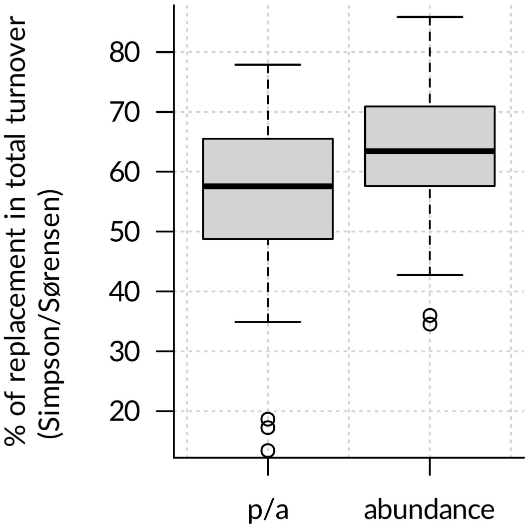

Figure A15: Share of replacement in total turnover for presence/absence and abundance-based calculation of indices, respectively. The share of replacement is calculated by dividing the Simpson dissimilarity by the Sørensen dissimilarity. For a definition of the replacement component, see Baselga (2010).

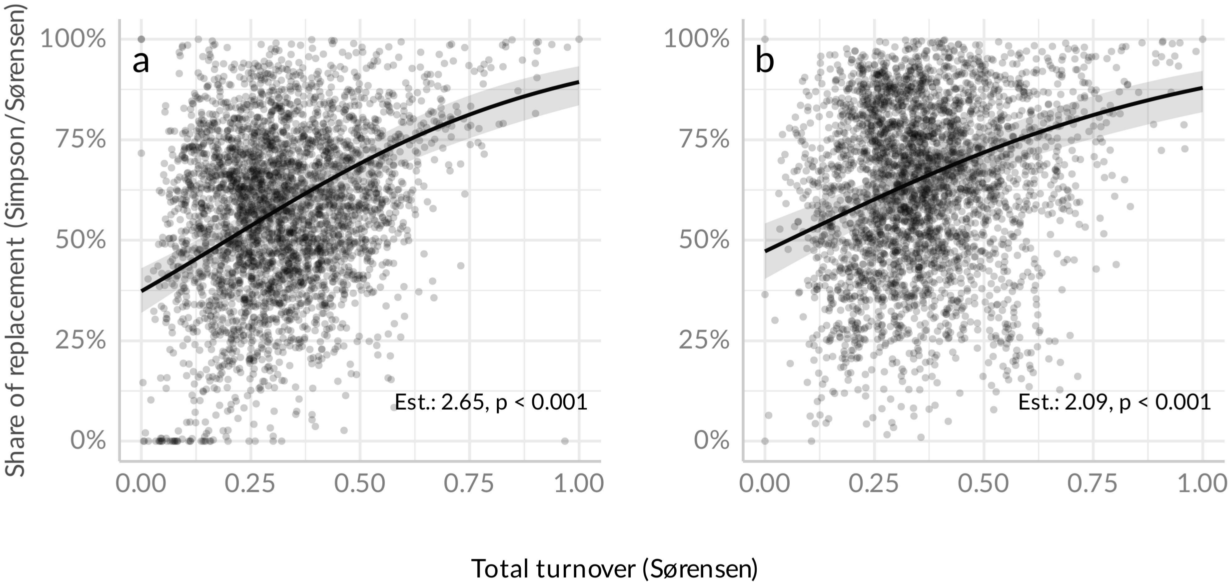

Figure A16: Share of replacement in total turnover, (a) presence/absence-based, (b) abundance-based. The share of replacement is calculated by dividing the Simpson dissimilarity by the Sørensen dissimilarity. For a definition of the replacement component, see Baselga (2010). Binomial models were fitted with a mixed model with “dataset” as random factor. Plotting of study-level effects by the function “ggpredict”.

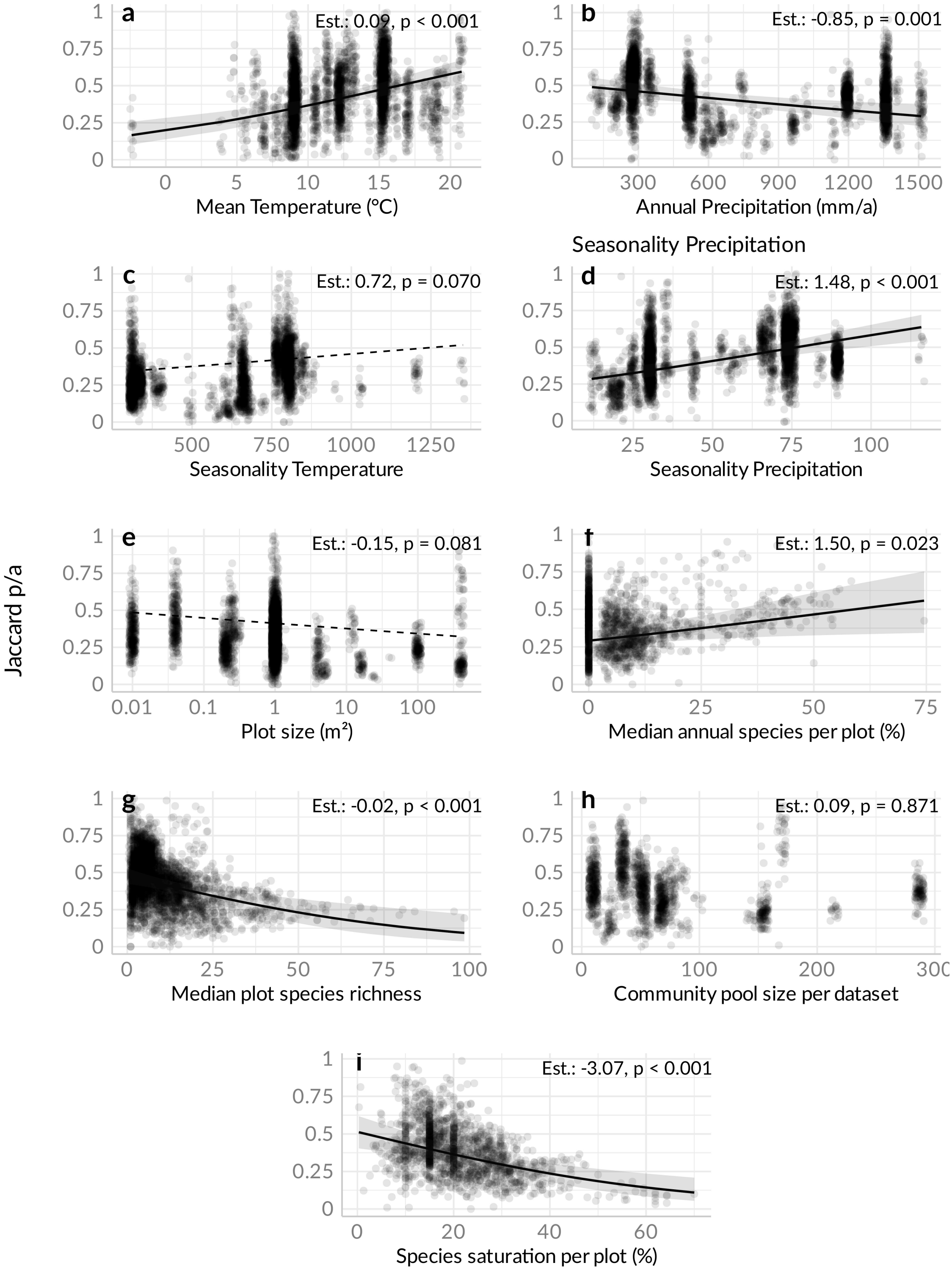

Figure A17: Simple mixed models showing the relationship between baseline turnover expressed using the **Jaccard dissimilarity index based on presence/absence data** and (a) mean annual temperature, (b) mean annual precipitation, (c) temperature seasonality (d) precipitation seasonality, (e) plot size (logarithmic scale), (f) median proportion of annual species per plot, (g) median species richness per plot, (h) community pool size, (i) species saturation per plot (median species richness/community pool). Trend lines represents results of logistic models at the population level (function "ggpredict"); dashed lines indicate significance levels between 0.05 and 0.1; strongly overlapping data points made visible by jittering (subplots a–e, h). See Figure 5.6, A18–A23 for corresponding results for the remaining seven dissimilarity indices.

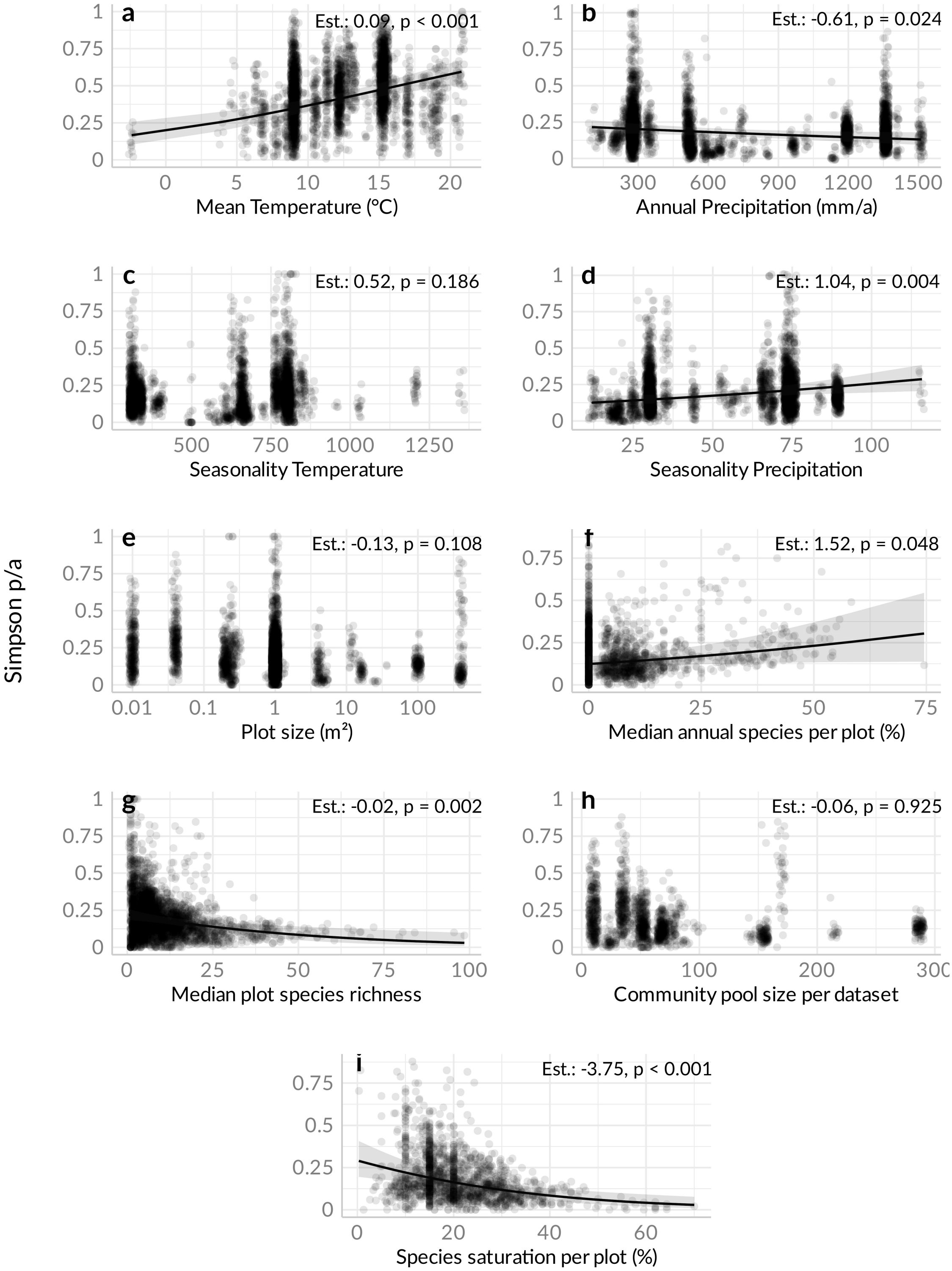

Figure A18: Simple mixed models showing the relationship between baseline turnover expressed using the **Simpson dissimilarity index based on presence/absence data** and (a) mean annual temperature, (b) mean annual precipitation, (c) temperature seasonality (d) precipitation seasonality, (e) plot size (logarithmic scale), (f) median proportion of annual species per plot, (g) median species richness per plot, (h) community pool size, (i) species saturation per plot (median species richness/community pool). Trend lines represents results of logistic models at the population level (function "ggpredict"); dashed lines indicate significance levels between 0.05 and 0.1; strongly overlapping data points made visible by jittering (subplots a–e, h). See Figure 5.6, A17, A19–A23 for corresponding results for the remaining seven dissimilarity indices.

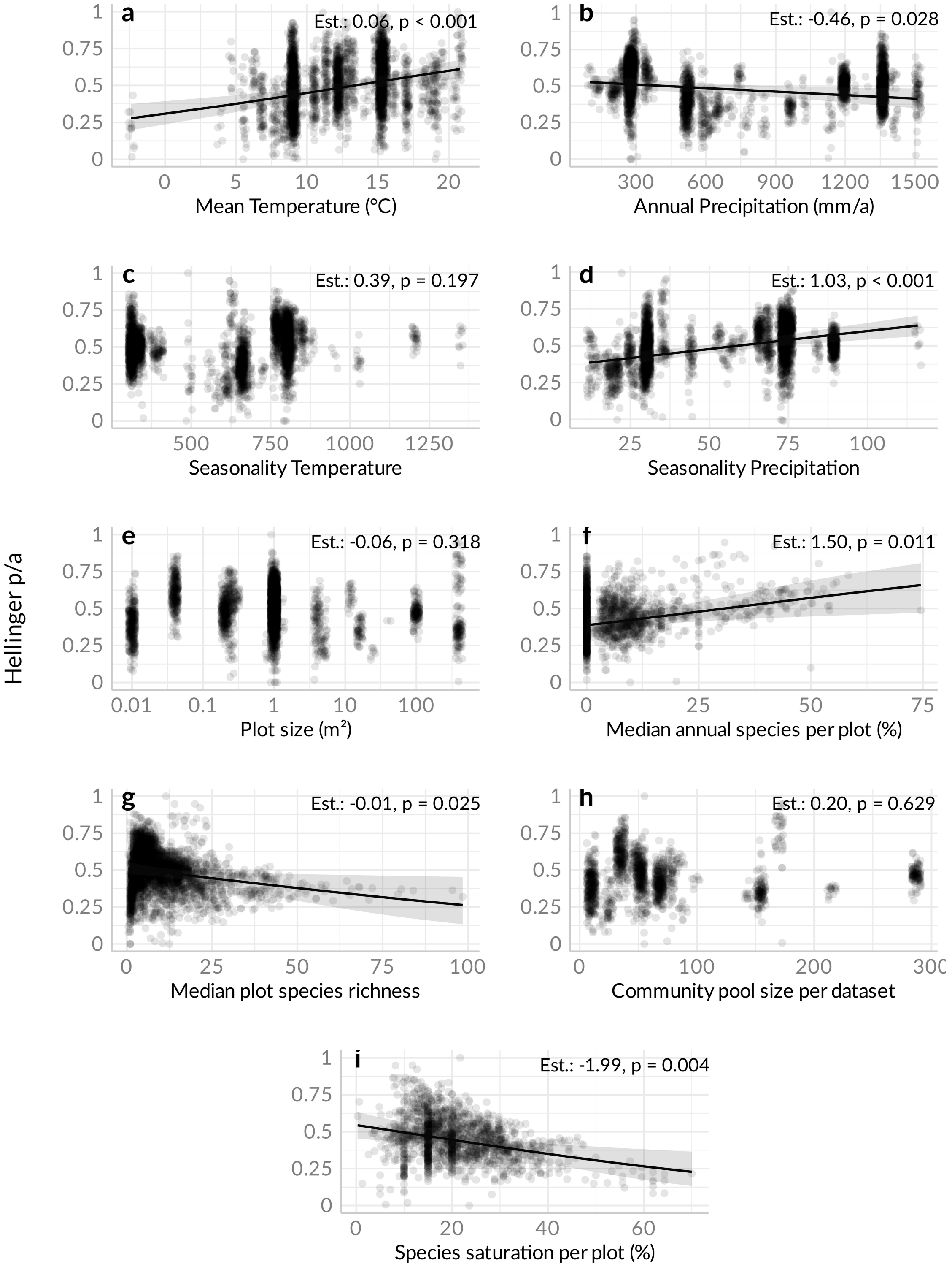

Figure A19: Simple mixed models showing the relationship between baseline turnover expressed using the **Hellinger dissimilarity index based on presence/absence data** and (a) mean annual temperature, (b) mean annual precipitation, (c) temperature seasonality (d) precipitation seasonality, (e) plot size (logarithmic scale), (f) median proportion of annual species per plot, (g) median species richness per plot, (h) community pool size, (i) species saturation per plot (median species richness/community pool). Trend lines represents results of logistic models at the population level (function “ggpredict”); dashed lines indicate significance levels between 0.05 and 0.1; strongly overlapping data points made visible by jittering (subplots a–e, h). See Figure 5.6, A8–A10, A7–A23 for corresponding results for the remaining seven dissimilarity indices.

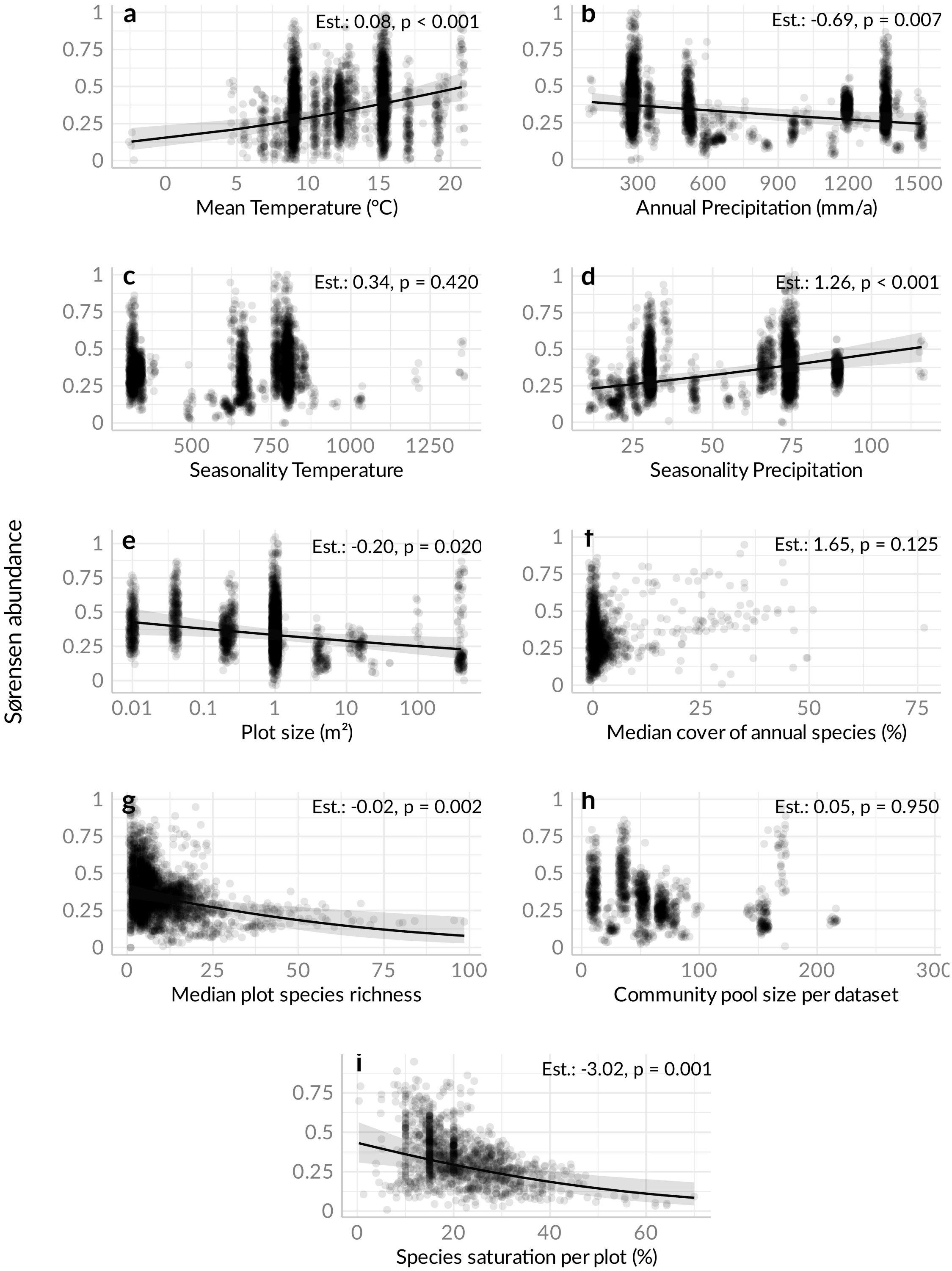

Figure A20: Simple mixed models showing the relationship between baseline turnover expressed using the **Sørensen dissimilarity index based on abundance data** and (a) mean annual temperature, (b) mean annual precipitation, (c) temperature seasonality (d) precipitation seasonality, (e) plot size (logarithmic scale), (f) median proportion of annual species per plot, (g) median species richness per plot, (h) community pool size, (i) species saturation per plot (median species richness/community pool). Trend lines represents results of logistic models at the population level (function "ggpredict"); dashed lines indicate significance levels between 0.05 and 0.1; strongly overlapping data points made visible by jittering (subplots a–e, h). See Figure 5.6, A17 – A19, A21–A23 for corresponding results for the remaining seven dissimilarity indices.

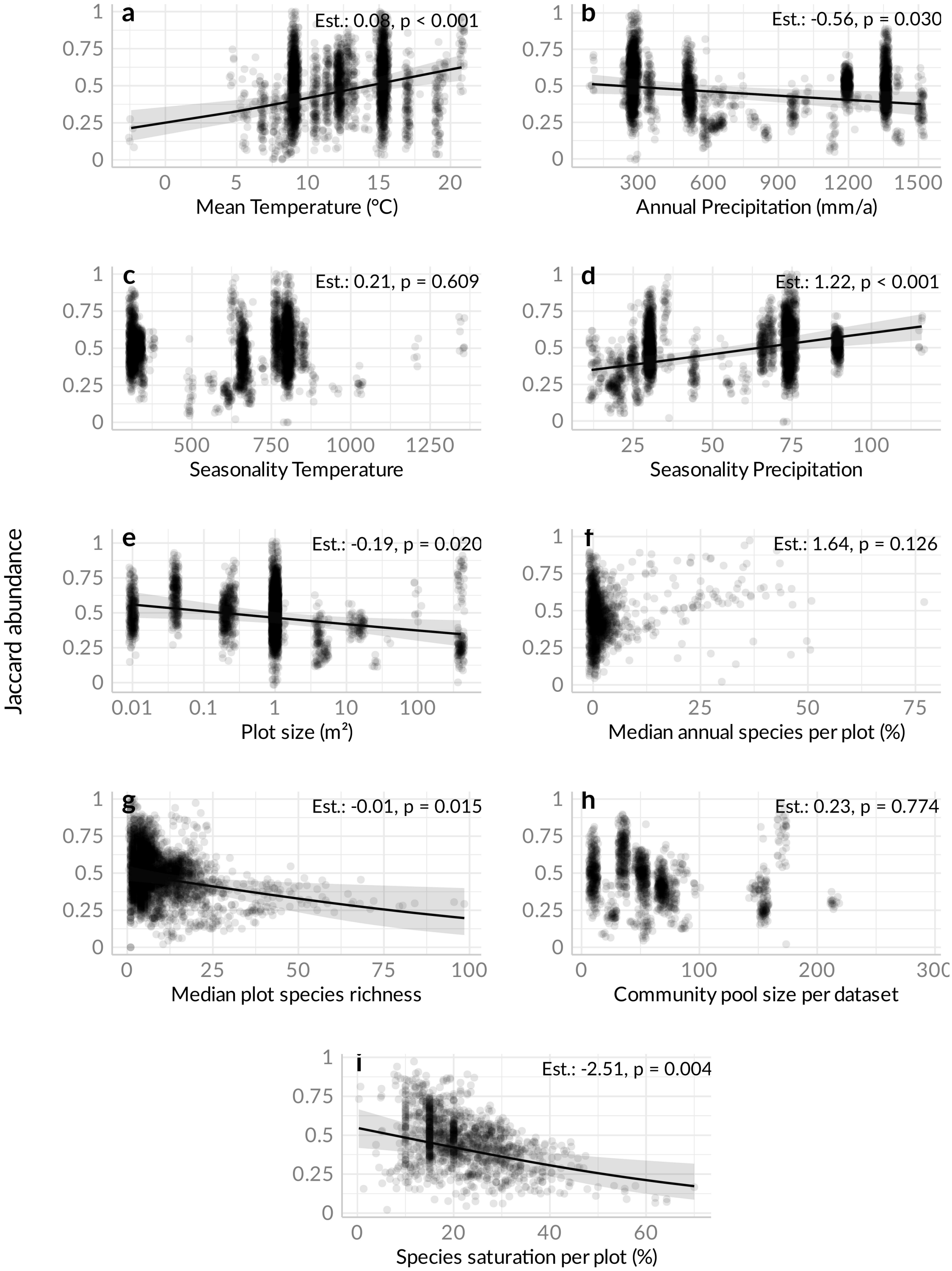

Figure A21: Simple mixed models showing the relationship between baseline turnover expressed using the **Jaccard dissimilarity index based on abundance data** and (a) mean annual temperature, (b) mean annual precipitation, (c) temperature seasonality (d) precipitation seasonality, (e) plot size (logarithmic scale), (f) median proportion of annual species per plot, (g) median species richness per plot, (h) community pool size, (i) species saturation per plot (median species richness/community pool). Trend lines represents results of logistic models at the population level (function "ggpredict"); dashed lines indicate significance levels between 0.05 and 0.1; strongly overlapping data points made visible by jittering (subplots a–e, h). See Figure 5.6, A17–A20, A22–A23 for corresponding results for the remaining seven dissimilarity indices.

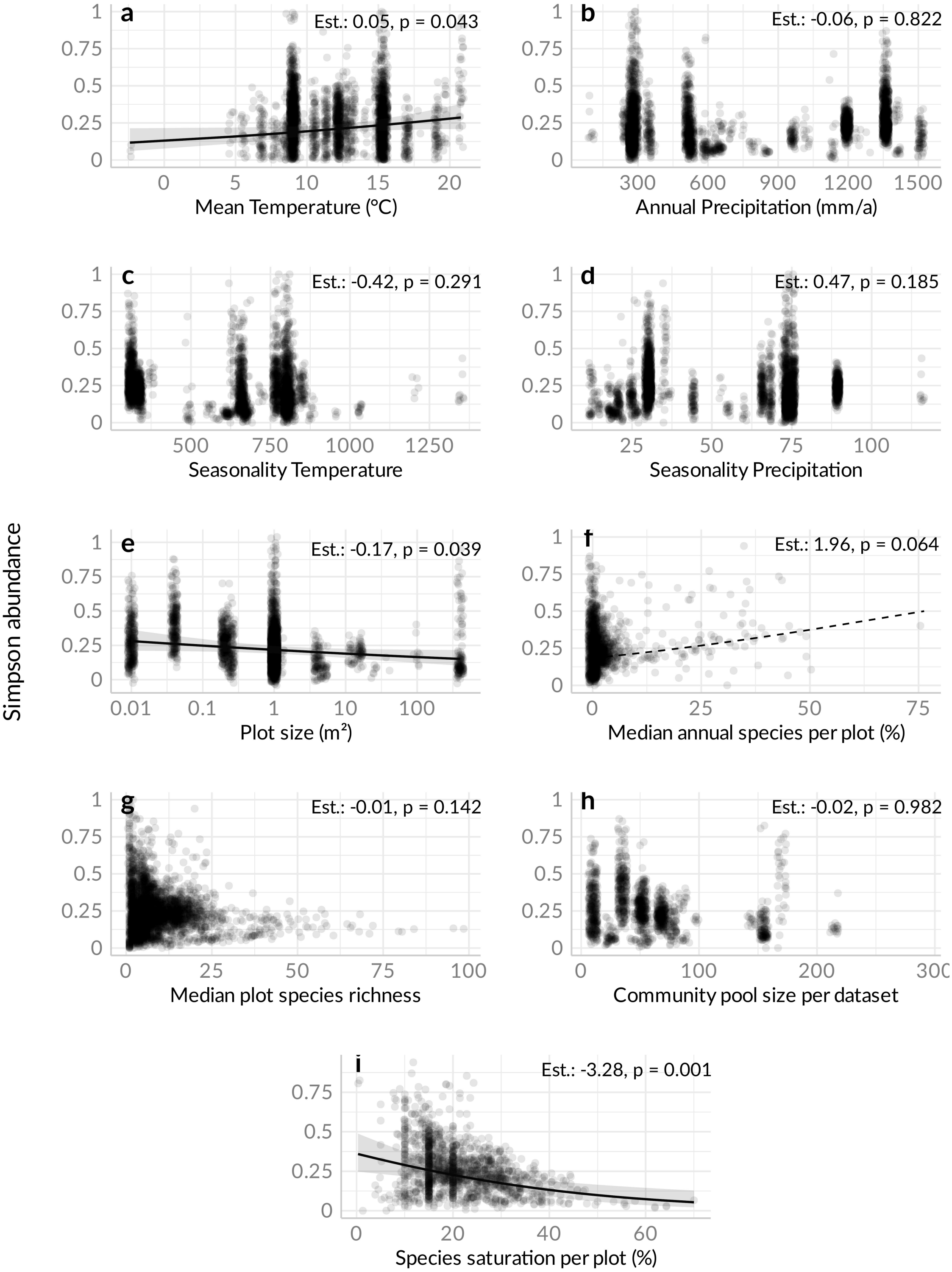

Figure A22: Simple mixed models showing the relationship between baseline turnover expressed using the **Simpson dissimilarity index based on abundance data** and (a) mean annual temperature, (b) mean annual precipitation, (c) temperature seasonality (d) precipitation seasonality, (e) plot size (logarithmic scale), (f) median proportion of annual species per plot, (g) median species richness per plot, (h) community pool size, (i) species saturation per plot (median species richness/community pool). Trend lines represents results of logistic models at the population level (function "ggpredict"); dashed lines indicate significance levels between 0.05 and 0.1; strongly overlapping data points made visible by jittering (subplots a–e, h). See Figure 5.6, A17–A21, A23 for corresponding results for the remaining seven dissimilarity indices.

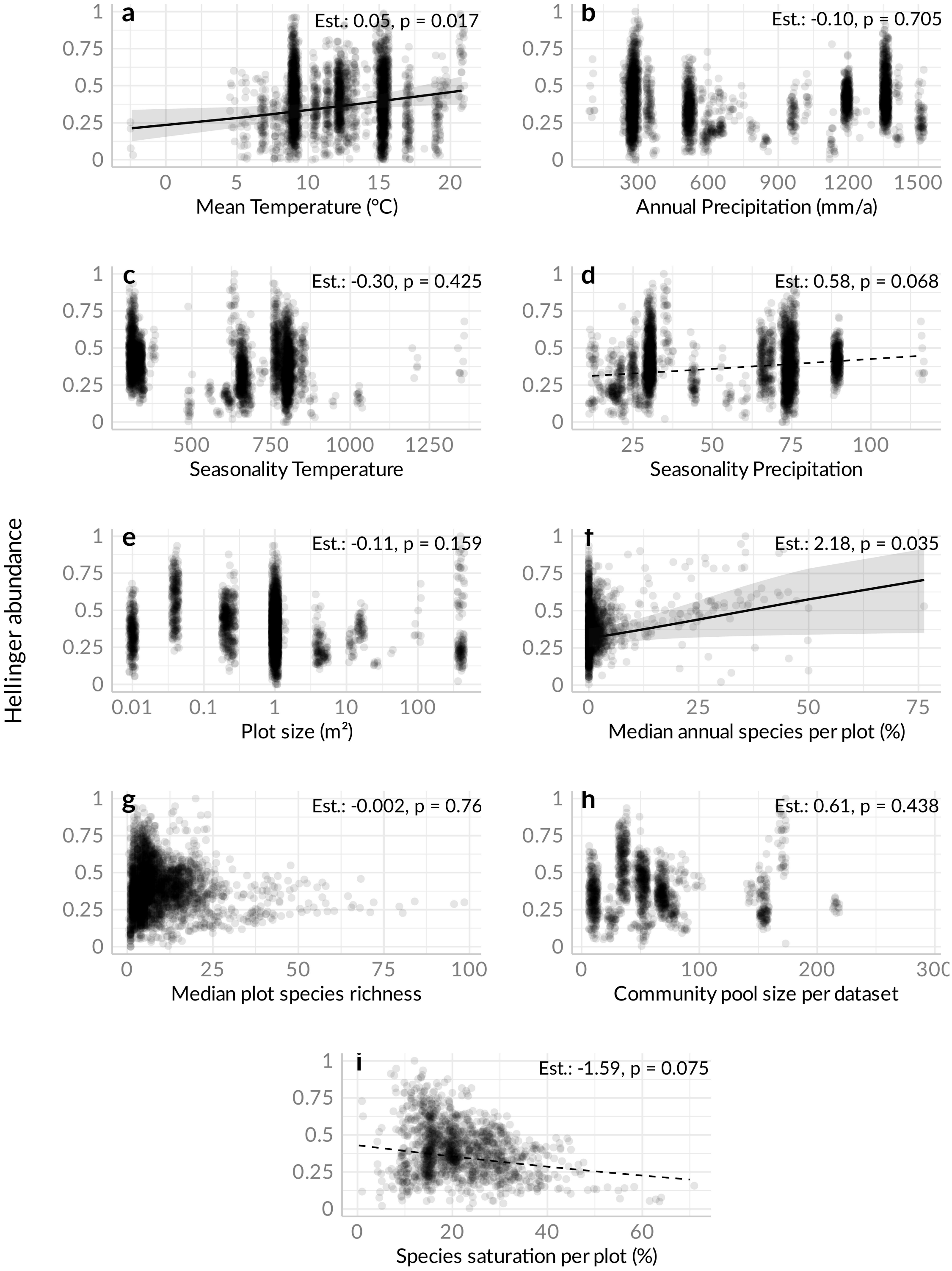

Figure A23: Simple mixed models showing the relationship between baseline turnover expressed using the **Hellinger dissimilarity index based on abundance data** and (a) mean annual temperature, (b) mean annual precipitation, (c) temperature seasonality (d) precipitation seasonality, (e) plot size (logarithmic scale), (f) median proportion of annual species per plot, (g) median species richness per plot, (h) community pool size, (i) species saturation per plot (median species richness/community pool). Trend lines represents results of logistic models at the population level (function "ggpredict"); dashed lines indicate significance levels between 0.05 and 0.1; strongly overlapping data points made visible by jittering (subplots a–e, h). See Figure 5.6, A17–A22 for corresponding results for the remaining seven dissimilarity indices.

Table A13: Computation formulae of the eight dissimilarity indices as given by Legendre & De Cáceres (2013) and derived from Chao et al. (2006) for the Simpson index. Where A = number of shared species between two plots, B = number of species unique to the first plot, C = number of species unique to the second plot, and y_{1j} = relative abundance of species j in the first plot, y_{2j} = relative abundance of species j in the second plot, p = number of total species.

Dissimilarity index	**Formula presence/absence-based**	**Formula abundance-based**
Sørensen index (Bray-Curtis index, percentage difference)	$\frac{B+C}{2A+B+C}$	$\frac{\sum_{j=1}^{p}\lvert y_{1j}-y_{2j}\rvert}{\sum_{j=1}^{p}(y_{1j}+y_{2j})}$ or $\frac{\sum_{j=1}^{p} y_{1j}+y_{2j}-2\cdot\left(\sum_{j=1}^{p} min(y_{1j},y_{2j})\right)}{\sum_{j=1}^{p} y_{1j}+y_{2j}}$
Jaccard index (abundance-based: Ružička index)	$\frac{B+C}{A+B+C}$	$1-\left(\frac{\sum_{j=1}^{p} y_{1j}y_{2j}}{\sum_{j=1}^{p} y_{1j}^2+\sum_{j=1}^{p} y_{2j}^2-\sum_{j=1}^{p} y_{1j}y_{2j}}\right)$ or $\frac{\sum_{j=1}^{p} y_{1j}+y_{2j}-2\cdot\left(\sum_{j=1}^{p} min(y_{1j},y_{2j})\right)}{\sum_{j=1}^{p} y_{1j}+y_{2j}-\sum_{j=1}^{p} min(y_{1j},y_{2j})}$
Simpson index (Lennon index, Overlap index)	$\frac{min(B,C)}{A+min(B,C)}$	$\frac{min\left(\sum_{j=1}^{p} y_{1j},\sum_{j=1}^{p} y_{2j}\right)-\sum_{j=1}^{p} min(y_{1j},y_{2j})}{min\left(\sum_{j=1}^{p} y_{1j},\sum_{j=1}^{p} y_{2j}\right)}$
Hellinger index	$\sqrt{2\cdot\left(1-\frac{A}{\sqrt{(A+B)\cdot(A+C)}}\right)}$	$\sqrt{\sum_{j=1}^{p}\left(\sqrt{\frac{y_{1j}}{\sum_{j=1}^{p} y_{1j}}}-\sqrt{\frac{y_{2j}}{\sum_{j=1}^{p} y_{2j}}}\right)^2}$

Table A14: Metadata and environmental data of the collected datasets.

Dataset name	Owner/ publication	Vegetation type	Plot size (m^2)	Koeppen/Geige climate classification	Location	n plots	Species richness per plot			Total species in dataset (community pool)	Saturation with species			Share of annual species per plot			Cover share of annual species per plot			Mean annual temperature			Sum of annual precipitation			Seasonality index temperature			Seasonality index precipitation		
							Mediar	25% quantile	75% quantile		Mediar	25% quantile	75% quantile	Mediar	25% quantile	75% quantile	Mediar	25% quantile	75% quantile	Mediar	25% quantile	75% quantile	Mediar	25% quantile	75% quantile	Mediar	25% quantile	75% quantile	Mediar	25% quantile	75% quantile
alpine vegetation																															
alpinegr	Michele Carbognani, Alessandro Petraglia, T'ai GW Forte	alpine primary grassland	1	Polar, tundra	Italy, Monte Gavia	5	13.0	13.0	13.5	21	0.62	0.62	0.64	0.04	0.04	0.04	0.00	0.00	0.00	-2.40	-2.40	-2.40	587.00	587.00	587.00	581.02	581.02	581.02	18.07	18.07	18.07
snowbed	Michele Carbognani, Alessandro Petraglia, T'ai GW Forte	alpine snowbeds	0.81	Polar, tundra	Italy, Passo del Gavia	10	12.5	11.6	13.0	22	0.53	0.57	0.59	0.08	0.04	0.09	NA	NA	NA	-2.40	-2.40	-2.40	587.00	587.00	587.00	581.02	581.02	581.02	18.07	18.07	18.07
deciduous forest																															
aelmoeseneiebos	Pieter deFrenne	ancient deciduous forest	0.25	Temperate, no dry season	Belgium, Gent	10	5.0	5.0	5.3	16	0.31	0.31	0.33	0.00	0.00	0.00	0.00	0.00	0.00	10.47	10.47	10.47	788.00	788.00	788.00	558.96	558.96	558.96	14.96	14.96	14.96
BEdeciduous	Schäfer, Deborah; Steffen Boch; Markus Fischer (2017): Vegetation Records for Forest EPs, 2009 - 2016. v1.4.5. Biodiversity Exploratories	beech forest, mature timber	400	Cold, no dry season	Germany, Schwäbische Alb	78	32.0	19.9	38.9	323	0.06	0.10	0.12	0.04	0.00	0.06	0.00	0.00	0.01	8.52	6.82	8.70	653.00	588.00	963.00	659.07	646.63	681.97	20.64	18.02	26.38
goe_control	Wolfgang Schmidt	Fagus forest, calcareous soil	25	Cold, no dry season	Germany, Göttingen	7	25.0	23.3	25.5	50	0.47	0.50	0.51	0.00	0.00	0.00	0.00	0.00	0.00	8.08	8.08	8.08	849.00	849.00	849.00	619.95	619.95	619.95	11.98	11.98	11.98
goe_subplots	Wolfgang Schmidt	Fagus forest, calcareous soil	1	Cold, no dry season	Germany, Göttingen	8	8.8	7.5	9.9	26	0.29	0.34	0.38	0.00	0.00	0.01	0.00	0.00	0.00	8.08	8.08	8.08	849.00	849.00	849.00	619.95	619.95	619.95	11.98	11.98	11.98
hardwood	Frank Gilliam	hardwood forest	5	Cold, no dry season	USA, W. Virginia	7	7.5	7.3	8.5	26	0.28	0.29	0.33	0.00	0.00	0.00	0.00	0.00	0.00	9.72	9.72	9.72	1240.00	1240.00	1240.00	840.38	840.38	840.38	14.08	14.08	14.08
stenshuvud	Jörg Brunet	ancient hornbeam forest	5	Cold, no dry season	south Sweden	30	8.0	7.1	9.0	39	0.18	0.21	0.23	0.00	0.00	0.00	0.00	0.00	0.00	7.70	7.70	7.70	621.00	621.00	621.00	607.47	607.47	607.47	19.47	19.47	19.47
desert vegetation																															
coolibah	John T. Hunter	Coolibah/Blackbox eucalyptus woodland	400	Arid, desert	East Australia, Naree & Yantabulla	34	19.5	15.3	21.4	315	0.05	0.06	0.07	0.29	0.22	0.35	0.27	0.15	0.35	20.78	20.78	20.78	295.00	295.00	295.00	629.87	629.87	629.87	35.34	35.34	35.34
dat_28	LOTVS (Sperandii et al. 2022)	desert grassland	1	Arid, desert	USA, New Mexico, Jornada Basin Experimental Range	64	2.0	2.0	3.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	14.92	14.92	14.92	279.00	279.00	279.00	795.90	795.90	795.90	72.48	72.48	72.48
dat_53.creo	LOTVS (Sperandii et al. 2022)	creosote shrubland	1	Arid, desert	USA, New Mexico, Jornada Basin Experimental Range	147	2.0	4.0	5.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15.22	15.22	15.22	273.00	273.00	273.00	801.23	801.23	801.23	73.50	73.50	73.50
dat_53.grama	LOTVS (Sperandii et al. 2022)	grama desert grassland	1	Arid, desert	USA, New Mexico, Jornada Basin Experimental Range	147	4.0	5.0	6.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15.22	15.22	15.22	273.00	273.00	273.00	801.23	801.23	801.23	73.50	73.50	73.50

Dataset name	**Owner/ publication**	**Vegetation type**	**Plot size (m²)**	**Koeppen/Geige climate classification**	**Location**	**n plots**	**Species richness per plot**			**Total species in dataset (community pool)**	**Saturation with species**			**Share of annual species per plot**			**Cover share of annual species per plot**			**Mean annual temperature**			**Sum of annual precipitation**			**Seasonality index temperature**			**Seasonality index precipitation**		
							Median	**25% quantile**	**75% quantile**		**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**
dat_53.mesq	LOTVS (Sperandii et al. 2022)	mesquite dunes	1	Arid, desert	USA, New Mexico, Jornada Basin Experimental Range	147	2.0	3.0	4.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15.22	15.22	15.22	273.00	273.00	273.00	801.23	801.23	801.23	73.50	73.50	73.50
dat_53.playa	LOTVS (Sperandii et al. 2022)	playa desert grassland	1	Arid, desert	USA, New Mexico, Jornada Basin Experimental Range	146	2.0	3.0	4.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15.22	15.22	15.22	273.00	273.00	273.00	801.23	801.23	801.23	73.50	73.50	73.50
dat_53.tarb	LOTVS (Sperandii et al. 2022)	tarbush shrubland	1	Arid, desert	USA, New Mexico, Jornada Basin Experimental Range	147	2.0	3.0	4.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15.22	15.22	15.22	273.00	273.00	273.00	801.23	801.23	801.23	73.50	73.50	73.50
dat_65.fall	LOTVS (Sperandii et al. 2022)	desert grassland	0.25	Arid, steppe	USA, New Mexico, Sevilleta National Wildlife Refuge	108	2.0	2.5	3.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12.72	12.72	12.72	275.00	275.00	275.00	819.19	819.19	819.19	68.27	68.27	68.27
dat_67.4	LOTVS (Sperandii et al. 2022)	black grama/creosote bush	12	Arid, desert	USA, New Mexico, Sevilleta National Wildlife Refuge	5	12.0	14.0	14.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	13.22	13.22	13.22	247.00	247.00	247.00	849.49	849.49	849.49	65.86	65.86	65.86
dat_67.5	LOTVS (Sperandii et al. 2022)	creosote shrubland	12	Arid, desert	USA, New Mexico, Sevilleta National Wildlife Refuge	5	8.0	9.0	9.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	13.22	13.22	13.22	247.00	247.00	247.00	849.49	849.49	849.49	65.86	65.86	65.86
dat_67.grama	LOTVS (Sperandii et al. 2022)	grama desert grassland	12	Arid, desert	USA, New Mexico, Sevilleta National Wildlife Refuge	15	7.0	8.0	8.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	13.22	13.22	13.22	247.00	247.00	247.00	849.49	849.49	849.49	65.86	65.86	65.86
dat_7.1	LOTVS (Sperandii et al. 2022)	desert shrubland (creosote)	1	Arid, desert	USA, New Mexico, Chihuahuan desert	140	3.0	4.0	5.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15.47	15.47	15.47	288.00	288.00	288.00	767.18	767.18	767.18	75.47	75.47	75.47
dat_7.2	LOTVS (Sperandii et al. 2022)	black grama desert grassland	1	Arid, desert	USA, New Mexico, Chihuahuan desert	144	5.0	6.0	7.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	15.47	15.47	15.47	288.00	288.00	288.00	767.18	767.18	767.18	75.47	75.47	75.47
dat_77	LOTVS (Sperandii et al. 2022)	montane desert steppe	100	Arid, desert	Mongolia, Gobi Gurvan Saykhan National Park	9	10.0	12.5	13.5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	4.68	4.68	4.68	101.00	101.00	101.00	1350.20	1350.20	1350.20	115.84	115.84	115.84
desertgr	Timothy Ohlert, Scott L. Collins	desert grassland	1	Arid, desert	USA, New Mexico	40	8.5	7.9	10.0	81	0.10	0.10	0.12	0.43	0.39	0.46	0.26	0.22	0.33	13.22	13.22	13.22	247.00	247.00	247.00	849.49	849.49	849.49	65.86	65.86	65.86
dune vegetation																															
dat_31	LOTVS (Sperandii et al. 2022)	dune grassland	1.25	Temperate, no dry season	USA, Virginia, Hog Island	14	4.0	4.3	5.4	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	14.15	14.15	14.15	1021.00	1021.00	1021.00	806.49	806.49	806.49	12.66	12.66	12.66
expmachair	Robin Pakeman	dune vegetation, dune top	1	Temperate, no dry season	Scotland, Western Isles	8	21.8	19.4	23.9	67	0.29	0.32	0.36	0.10	0.08	0.12	0.02	0.01	0.03	8.95	8.95	8.95	1360.00	1360.00	1360.00	313.84	313.84	313.84	30.56	30.56	30.56
machair004	Robin Pakeman	dune grassland	0.04	Temperate, no dry season	Scotland, Western Isles	250	5.5	5.0	6.5	73	0.07	0.08	0.09	0.00	0.00	0.00	0.00	0.00	0.00	8.97	8.97	8.97	1360.00	1360.00	1360.00	312.20	312.20	312.20	30.38	30.38	30.38
machair02	Robin Pakeman	dune grassland	0.2	Temperate, no dry season	Scotland, Western Isles	250	11.0	9.5	13.8	99	0.10	0.11	0.14	0.06	0.04	0.09	0.01	0.01	0.02	8.97	8.97	8.97	1360.00	1360.00	1360.00	312.20	312.20	312.20	30.38	30.38	30.38
machair1	Robin Pakeman	dune grassland	1	Temperate, no dry season	Scotland, Western Isles	250	18.5	15.3	20.8	125	0.12	0.15	0.17	0.10	0.08	0.12	0.02	0.02	0.03	8.97	8.97	8.97	1360.00	1360.00	1360.00	312.20	312.20	312.20	30.38	30.38	30.38
evergreen forest																															

Dataset name	Owner/ publication	Vegetation type	Plot size (m²)	Koeppen/Geige climate classification	Location	n plots	Species richness per plot			Total species in dataset (community pool)	Saturation with species			Share of annual species per plot			Cover share of annual species per plot			Mean annual temperature			Sum of annual precipitation			Seasonality index temperature			Seasonality index precipitation		
							Median	25% quantile	75% quantile		Median	25% quantile	75% quantile	Median	25% quantile	75% quantile	Median	25% quantile	75% quantile	Median	25% quantile	75% quantile	Median	25% quantile	75% quantile	Median	25% quantile	75% quantile	Median	25% quantile	75% quantile
BEpine	Schäfer, Deborah; Steffen Boch; Markus Fischer (2017): Vegetation Records for Forest EPs, 2009–2016. v1.4.5. Biodiversity Exploratories	pine forest, immature timber	400	Cold, no dry season	Germany, Schorfheide-Chorin	11	26.5	22.5	29.5	115	0.20	0.23	0.26	0.05	0.00	0.06	0.00	0.00	0.00	8.70	8.70	8.70	588.00	588.00	588.00	681.97	681.97	681.97	26.38	26.38	26.38
BEspruce	Schäfer, Deborah; Steffen Boch; Markus Fischer (2017): Vegetation Records for Forest EPs, 2009–2016. v1.4.5. Biodiversity Exploratories	spruce forest, immature timber	400	Cold, no dry season	Germany, Schwäbische Alb	16	67.0	57.8	79.8	300	0.19	0.22	0.27	0.09	0.07	0.11	0.06	0.04	0.08	6.82	6.82	7.25	963.00	885.50	963.00	659.07	655.96	659.07	20.64	19.99	20.64
steppe/prairie																															
dat_12	LOTVS (Sperandii et al. 2022)	forest steppe	1	Cold, no dry season	Hungary, Kiskunság National Park	100	5.0	6.5	8.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	10.51	10.51	10.51	525.50	525.50	525.50	809.26	809.26	809.26	24.74	24.74	24.74
dat_13	LOTVS (Sperandii et al. 2022)	sand prairie	1	Cold, no dry season	USA, Minnesota, Cedar Creek Ecosystem Science Reserve	5	8.0	9.0	10.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	6.29	6.29	6.29	744.00	744.00	744.00	1205.09	1205.09	1205.09	52.79	52.79	52.79
dat_16	LOTVS (Sperandii et al. 2022)	sand prairie	0.3	Cold, no dry season	USA, Minnesota, Cedar Creek Ecosystem Science Reserve	23	7.5	10.0	12.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	6.29	6.29	6.29	744.00	744.00	744.00	1205.09	1205.09	1205.09	52.79	52.79	52.79
dat_2	LOTVS (Sperandii et al. 2022)	shortgrass prairie	1	Cold, no dry season	USA, Kansas, Hays	15	4.0	4.0	5.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12.11	12.11	12.11	586.00	586.00	586.00	1027.94	1027.94	1027.94	55.11	55.11	55.11
dat_3	LOTVS (Sperandii et al. 2022)	shortgrass prairie	1	Arid, steppe	USA, Colorado, Nunn, Central Plains Experimental Range	12	7.0	8.0	10.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	8.99	8.99	8.99	367.00	367.00	367.00	879.53	879.53	879.53	60.19	60.19	60.19
dat_4	LOTVS (Sperandii et al. 2022)	semi-desert grasslands	1	Arid, steppe	USA, Arizona, Santa Rita Experimental Range	109	3.5	4.0	5.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	17.01	17.01	17.01	528.00	528.00	528.00	669.57	669.57	669.57	75.18	75.18	75.18
dat_5	LOTVS (Sperandii et al. 2022)	Sagebrush steppe	1	Arid, steppe	USA, Idaho	4	14.5	15.5	16.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5.47	5.47	5.47	297.00	297.00	297.00	952.69	952.69	952.69	28.97	28.97	28.97
dat_66.fall	LOTVS (Sperandii et al. 2022)	pinon-juniper woodland	1	Arid, steppe	USA, New Mexico, Sevilleta National Wildlife Refuge	100	5.0	6.0	7.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	11.38	11.38	11.38	346.00	346.00	346.00	781.29	781.29	781.29	65.74	65.74	65.74
succulent desert vegetation																															
kalaha	Ute Schmiedel	Kalahari desert	100	Arid, desert	South Africa	20	10.8	7.4	13.0	73	0.10	0.15	0.18	0.32	0.30	0.35	NA	NA	NA	20.49	20.49	20.49	206.00	206.00	206.00	605.26	605.26	605.26	83.94	83.94	83.94
karoo	Ute Schmiedel	Succulent Karoo	100	Arid, desert	South Africa	104	27.8	23.0	34.0	709	0.03	0.04	0.05	0.22	0.14	0.36	NA	NA	NA	18.19	16.10	18.69	195.00	195.00	220.00	388.24	388.24	403.57	57.06	35.45	68.99

Dataset name	**Owner/ publication**	**Vegetation type**	**Plot size (m^2)**	**Koeppen/Geige climate classification**	**Location**	**n plots**	**Species richness per plot**			**Total species in dataset (community pool)**	**Saturation with species**			**Share of annual species per plot**			**Cover share of annual species per plot**			**Mean annual temperature**			**Sum of annual precipitation**			**Seasonality index temperature**			**Seasonality index precipitation**		
							Median	**25% quantile**	**75% quantile**		**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**
temperate grassland																																		
BEgrass_chalk	Schäfer, Deborah; Daniel Prati; Markus Fischer; Norbert Hoelzel (2018): Vegetation Records for Grassland EPs, 2008–2017. v1.3.1. Biodiversity Exploratories Information System. Dataset. Link to Dataset	chalk grassland	16	Cold, no dry season	Germany, Schwäbische Alb	13	44.8	43.0	48.8	177	0.24	0.25	0.28	0.06	0.04	0.08	0.02	0.01	0.02	6.82	6.82	6.82	963.00	963.00	963.00	659.07	659.07	659.07	20.64	20.64	20.64
BEgrass_ mesicchalk	Schäfer, Deborah; Daniel Prati; Markus Fischer; Norbert Hoelzel (2018): Vegetation Records for Grassland EPs, 2008 - 2017. v1.3.1. Biodiversity Exploratories Information System. Dataset. Link to Dataset	mesic chalk grassland	16	Cold, no dry season	Germany, Schwäbische Alb	34	34.5	28.5	41.0	243	0.12	0.14	0.17	0.08	0.04	0.10	0.02	0.00	0.04	6.82	6.82	8.52	963.00	653.00	963.00	659.07	646.63	659.07	20.64	18.02	20.64
campos025	Felicia M. Fischer, Valerio D. Pillar, Daniela Hoss	Brazilian native campos grassland	0.25	Temperate, no dry season	Brazil, Eldorado do Sul municipality	15	23.5	22.0	25.0	122	0.18	0.19	0.20	0.05	0.04	0.06	0.01	0.01	0.01	19.60	19.60	19.60	1407.00	1407.00	1407.00	376.07	376.07	376.07	12.18	12.18	12.18
coastheadlands	John T. Hunter	Themeda grassland on headlands	4	Temperate, no dry season	Australia, East Coast	74	10.4	8.6	12.9	261	0.03	0.04	0.05	0.03	0.00	0.08	0.00	0.00	0.01	19.09	19.09	19.09	1511.00	1511.00	1511.00	340.57	340.57	340.57	44.13	44.13	44.13
dat_27.1	LOTVS (Sperandii et al. 2022)	non serpentine grassland	1	Temperate, dry summer	USA, California	205	8.0	10.5	13.5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12.19	12.19	12.19	1194.00	1194.00	1194.00	334.55	334.55	334.55	89.30	89.30	89.30
dat_27.2	LOTVS (Sperandii et al. 2022)	serpentine grassland	1	Temperate, dry summer	USA, California	195	12.0	14.0	16.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	12.19	12.19	12.19	1194.00	1194.00	1194.00	334.55	334.55	334.55	89.30	89.30	89.30
dat_29	LOTVS (Sperandii et al. 2022)	montane Nardus grassland	0.25	Cold, no dry season	Czech Republic, Krkonose Mountains	4	7.8	9.0	10.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.85	3.85	3.85	762.00	762.00	762.00	672.08	672.08	672.08	31.91	31.91	31.91
dat_30	LOTVS (Sperandii et al. 2022)	montane Nardus grassland	0.25	Cold, no dry season	Czech Republic, Krkonose Mountains	4	26.8	28.0	29.1	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	3.85	3.85	3.85	762.00	762.00	762.00	672.08	672.08	672.08	31.91	31.91	31.91
dat_39	LOTVS (Sperandii et al. 2022)	wet poor meadow	0.25	Cold, no dry season	Czech Republic, Ohrazeni	3	33.3	33.5	34.3	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	7.72	7.72	7.72	711.00	711.00	711.00	721.04	721.04	721.04	31.08	31.08	31.08
dat_70	LOTVS (Sperandii et al. 2022)	mesic seminatural grassland	1	Cold, no dry season	Czech Republic, Zvíkov	10	23.9	27.3	28.0	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	7.76	7.76	7.76	702.00	702.00	702.00	722.80	722.80	722.80	31.15	31.15	31.15

Dataset name	**Owner/ publication**	**Vegetation type**	**Plot size (m^2)**	**Koeppen/Geige climate classification**	**Location**	**n plots**	**Species richness per plot**			**Total species in dataset (community pool)**	**Saturation with species**			**Share of annual species per plot**			**Cover share of annual species per plot**			**Mean annual temperature**			**Sum of annual precipitation**			**Seasonality index temperature**			**Seasonality index precipitation**		
							Median	**25% quantile**	**75% quantile**		**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**	**Median**	**25% quantile**	**75% quantile**
dat_79	LOTVS (Sperandii et al. 2022)	mesic semi-natural grassland	0.25	Cold, no dry season	Estonia, Ahja River	7	12.5	15.0	15.5	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	5.45	5.45	5.45	620.00	620.00	620.00	855.59	855.59	855.59	34.04	34.04	34.04
devin	Jiří Danihelka	dry grassland	16	Cold, no dry season	Czech Republic, Děvín Hill, Pavlov Hills	7	42.5	41.3	43.5	120	0.34	0.35	0.36	0.32	0.30	0.36	0.14	0.12	0.18	9.13	9.13	9.13	574.00	574.00	574.00	768.18	768.18	768.18	36.67	36.67	36.67
harz	Cord Peppler-Lisbach, Hartmut Dierschke	poor mountain meadow	4	Cold, no dry season	Germany, Harz	14	21.3	20.1	23.8	71	0.28	0.30	0.33	0.00	0.00	0.02	0.00	0.00	0.00	5.62	5.62	5.62	1413.00	1413.00	1413.00	619.83	619.83	619.83	20.27	20.27	20.27
ossekampen	Berendse et al. (2021). A matter of time: recovery of plant species diversity in wild plant communities at declining nitrogen deposition. *Diversity and Distributions* 27: 1180–1193.	mesic meadow, mown	40	Temperate, no dry season	Netherlands, Wageningen	2	29.3	28.1	30.4	78	0.36	0.38	0.39	0.00	0.00	0.00	0.00	0.00	0.00	9.69	9.69	9.69	800.00	800.00	800.00	557.91	557.91	557.91	14.90	14.90	14.90
xerogr	Silvia Matesanz, Rob Brooker, Stefan Klotz	xerothermic grassland	1	Cold, no dry season	Germany, Halle	3	9.5	9.5	9.5	35	0.27	0.27	0.27	0.16	0.16	0.16	0.01	0.01	0.01	9.17	9.17	9.17	513.00	513.00	513.00	658.14	658.14	658.14	29.60	29.60	29.60
xerogr_sub	Silvia Matesanz, Rob Brooker, Stefan Klotz	xerothermic grassland	0.01	Cold, no dry season	*Germany, Halle*	300	1.5	1.5	2.0	35	0.04	0.04	0.06	0.00	0.00	0.00	0.00	0.00	0.00	9.17	9.17	9.17	513.00	513.00	513.00	658.14	658.14	658.14	29.60	29.60	29.60
mire																															
mire	Idoia Biurrun, Juan A. Campos	mire	1	Temperate, no dry season	Spain, Navarra	22	12.5	11.6	14.9	65	0.18	0.19	0.23	0.03	0.00	0.08	0.00	0.00	0.01	11.22	11.22	11.22	1133.00	1133.00	1133.00	493.22	493.22	493.22	21.57	21.57	21.57

Table A15: Detailed values of baseline turnover per dataset: median, 25 %- and 75 %-quantile for all eight dissimilarity indices. Datasets are grouped into vegetation categories and their mean values are given as well. Datasets set in italics and grey colour were not used in the calculation of vegetation type means due to their very small (and rather unusual) plot sizes (< 0.25 m^2).

Dataset name	**Vegetation type**	**Plot size (m^2)**	**Location**	**n plots**	**Sørensen index**						**Jaccard index**						**Simpson index**						**Hellinger index**					
					p/a Median	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**	**p/a Median**	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**	**p/a Median**	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**	**p/a Median**	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**
alpine vegetation																												
alpinegr	alpine primary grassland	1	Italy, Monte Gavia	5	0.03	0.02	0.03	0.05	0.04	0.05	0.05	0.04	0.06	0.09	0.07	0.09	0.00	0.00	0.01	0.03	0.03	0.03	0.17	0.12	0.18	0.09	0.07	0.09
snowbed	alpine snowbeds	0.81	Italy, Passo del Gavia	10	0.06	0.05	0.09	NA	NA	NA	0.11	0.09	0.16	NA	NA	NA	0.04	0.01	0.05	NA	NA	NA	0.29	0.24	0.38	NA	NA	NA
					Ø 0.04	**0.04**	**0.06**	**0.05**	**0.04**	**0.05**	**0.08**	**0.07**	**0.11**	**0.09**	**0.07**	**0.09**	**0.02**	**0.01**	**0.03**	**0.03**	**0.03**	**0.03**	**0.23**	**0.18**	**0.28**	**0.09**	**0.07**	**0.09**
deciduous forest																												
aelmoeseneiebos	ancient deciduous forest	0.25	Belgium, Gent	10	0.16	0.12	0.21	0.17	0.16	0.18	0.25	0.20	0.31	0.28	0.26	0.29	0.06	0.04	0.10	0.10	0.08	0.12	0.46	0.38	0.53	0.29	0.26	0.32
BEdeciduous	beech forest, mature timber	400	Germany, Schwäbische Alb	78	0.13	0.11	0.16	0.15	0.13	0.17	0.23	0.19	0.26	0.25	0.23	0.28	0.07	0.05	0.11	0.09	0.07	0.12	0.49	0.44	0.53	0.30	0.25	0.34
goe_control	Fagus forest, calcareous soil	25	Germany, Göttingen	7	0.05	0.04	0.06	0.09	0.09	0.10	0.09	0.08	0.10	0.17	0.16	0.17	0.02	0.02	0.03	0.06	0.05	0.06	0.29	0.26	0.32	0.19	0.18	0.20
goe_subplots	Fagus forest, calcareous soil	1	Germany, Göttingen	8	0.12	0.09	0.19	0.11	0.09	0.11	0.20	0.16	0.32	0.19	0.17	0.20	0.06	0.04	0.11	0.06	0.05	0.07	0.43	0.37	0.61	0.15	0.13	0.17
hardwood	hardwood forest	5	USA, W. Virginia	7	0.24	0.18	0.26	0.26	0.24	0.27	0.36	0.29	0.40	0.41	0.37	0.42	0.13	0.10	0.20	0.15	0.14	0.19	0.62	0.55	0.69	0.43	0.37	0.45
stenshuvud	ancient hornbeam forest	5	south Sweden	30	0.08	0.07	0.10	0.13	0.11	0.14	0.15	0.12	0.18	0.22	0.20	0.24	0.03	0.03	0.04	0.06	0.05	0.07	0.32	0.28	0.41	0.26	0.25	0.28
					Ø 0.13	**0.10**	**0.16**	**0.15**	**0.14**	**0.16**	**0.21**	**0.17**	**0.26**	**0.25**	**0.23**	**0.27**	**0.06**	**0.05**	**0.10**	**0.09**	**0.07**	**0.11**	**0.44**	**0.38**	**0.52**	**0.27**	**0.24**	**0.29**
desert vegetation																												
coolibah	Coolibah/Blackbox eucalyptus woodland	400	East Australia, Naree & Yantabulla	34	0.60	0.47	0.72	0.66	0.49	0.73	0.74	0.63	0.84	0.78	0.65	0.84	0.49	0.30	0.59	0.49	0.34	0.64	1.08	0.94	1.18	0.96	0.75	1.10
dat_28	desert grassland	1	USA, New Mexico, Jornada Basin Experimental Range	64	0.48	0.37	0.58	0.53	0.42	0.61	0.60	0.48	0.68	0.64	0.54	0.72	0.33	0.19	0.42	0.37	0.22	0.45	0.87	0.72	1.00	0.84	0.68	0.95
dat_53.creo	creosote shrubland	1	USA, New Mexico, Jornada Basin Experimental Range	147	0.35	0.27	0.47	0.29	0.19	0.47	0.49	0.38	0.60	0.43	0.30	0.61	0.16	0.10	0.26	0.12	0.07	0.27	0.74	0.59	0.85	0.35	0.21	0.56
dat_53.grama	grama desert grassland	1	USA, New Mexico, Jornada Basin Experimental Range	147	0.49	0.42	0.54	0.41	0.31	0.47	0.63	0.57	0.68	0.55	0.45	0.62	0.27	0.21	0.33	0.20	0.16	0.28	0.93	0.85	0.99	0.54	0.40	0.67
dat_53.mesq	mesquite dunes	1	USA, New Mexico, Jornada Basin Experimental Range	147	0.45	0.39	0.52	0.47	0.31	0.61	0.58	0.50	0.64	0.59	0.44	0.71	0.28	0.18	0.44	0.31	0.15	0.47	0.80	0.65	0.89	0.54	0.37	0.73
dat_53.playa	playa desert grassland	1	USA, New Mexico, Jornada Basin Experimental Range	146	0.37	0.33	0.41	0.53	0.45	0.57	0.50	0.44	0.53	0.65	0.57	0.69	0.16	0.12	0.20	0.16	0.13	0.22	0.73	0.63	0.80	0.44	0.38	0.58
dat_53.tarb	tarbush shrubland	1	USA, New Mexico, Jornada Basin Experimental Range	147	0.31	0.25	0.40	0.33	0.23	0.42	0.45	0.37	0.53	0.45	0.35	0.54	0.15	0.09	0.20	0.12	0.09	0.18	0.69	0.59	0.76	0.35	0.26	0.46
dat_65.fall	desert grassland	0.25	USA, New Mexico, Sevilleta National Wildlife Refuge	108	0.42	0.34	0.54	0.43	0.33	0.53	0.57	0.47	0.66	0.58	0.49	0.66	0.20	0.09	0.32	0.18	0.11	0.33	0.81	0.69	0.93	0.57	0.40	0.68
dat_67.4	black grama/ creosote bush	12	USA, New Mexico, Sevilleta National Wildlife Refuge	5	0.31	0.29	0.34	0.25	0.24	0.25	0.47	0.44	0.50	0.39	0.38	0.40	0.21	0.18	0.21	0.17	0.16	0.18	0.76	0.74	0.79	0.37	0.36	0.40
dat_67.5	creosote shrubland	12	USA, New Mexico, Sevilleta National Wildlife Refuge	5	0.30	0.30	0.35	0.29	0.28	0.29	0.45	0.44	0.51	0.44	0.43	0.45	0.20	0.14	0.21	0.17	0.17	0.21	0.75	0.72	0.81	0.41	0.39	0.42
dat_67.grama	grama desert grassland	12	USA, New Mexico, Sevilleta National Wildlife Refuge	15	0.44	0.40	0.46	0.32	0.25	0.36	0.58	0.55	0.62	0.43	0.39	0.49	0.29	0.26	0.33	0.19	0.16	0.24	0.89	0.82	0.92	0.34	0.28	0.40
dat_7.1	desert shrubland (creosote)	1	USA, New Mexico, Chihuahuan desert	140	0.43	0.35	0.54	0.42	0.30	0.67	0.56	0.47	0.68	0.58	0.45	0.77	0.23	0.15	0.35	0.23	0.14	0.40	0.84	0.73	0.95	0.58	0.42	0.84
dat_7.2	black grama desert grassland	1	USA, New Mexico, Chihuahuan desert	144	0.47	0.42	0.52	0.44	0.37	0.51	0.62	0.58	0.66	0.60	0.53	0.66	0.25	0.19	0.31	0.30	0.23	0.36	0.92	0.87	0.96	0.67	0.54	0.80
dat_77	montane desert steppe	100	Mongolia, Gobi Gurvan Saykhan National Park	9	0.35	0.27	0.40	0.35	0.34	0.53	0.51	0.41	0.56	0.51	0.50	0.68	0.20	0.13	0.25	0.17	0.15	0.19	0.82	0.71	0.86	0.45	0.45	0.68

Dataset name	**Vegetation type**	**Plot size (m^2)**	**Location**	**n plots**	**Sørensen index**						**Jaccard index**						**Simpson index**						**Hellinger index**					
					p/a Median	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**	**p/a Median**	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**	**p/a Median**	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**	**p/a Median**	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**
desertgr	desert grassland	1	USA, New Mexico	40	0.39	0.35	0.42	0.42	0.37	0.46	0.54	0.49	0.58	0.57	0.52	0.60	0.28	0.23	0.32	0.28	0.23	0.31	0.85	0.78	0.89	0.69	0.61	0.75
					Ø 0.41	**0.35**	**0.48**	**0.41**	**0.33**	**0.50**	**0.55**	**0.48**	**0.62**	**0.55**	**0.47**	**0.63**	**0.25**	**0.17**	**0.32**	**0.23**	**0.17**	**0.31**	**0.83**	**0.73**	**0.91**	**0.54**	**0.43**	**0.67**
dune vegetation																												
dat_31	dune grassland	1.25	USA, Virginia, Hog Island	14	0.21	0.18	0.25	0.26	0.24	0.30	0.31	0.27	0.37	0.39	0.36	0.44	0.13	0.08	0.17	0.16	0.13	0.21	0.53	0.50	0.60	0.56	0.50	0.58
expmachair	dune vegetation, dune top	1	Scotland, Western Isles	8	0.19	0.17	0.19	0.25	0.22	0.30	0.30	0.28	0.31	0.39	0.36	0.46	0.11	0.09	0.13	0.18	0.16	0.21	0.58	0.55	0.60	0.46	0.42	0.53
machair004	*dune grassland*	*0.04*	Scotland, Western Isles	250	*0.41*	*0.33*	*0.52*	*0.48*	*0.37*	*0.58*	*0.56*	*0.48*	*0.67*	*0.63*	*0.53*	*0.72*	*0.28*	*0.20*	*0.36*	*0.39*	*0.29*	*0.48*	*0.87*	*0.77*	*0.96*	*0.80*	*0.61*	*0.94*
machair02	*dune grassland*	*0.2*	Scotland, Western Isles	250	*0.25*	*0.19*	*0.30*	*0.33*	*0.27*	*0.38*	*0.39*	*0.31*	*0.45*	*0.49*	*0.43*	*0.54*	*0.15*	*0.11*	*0.22*	*0.27*	*0.21*	*0.33*	*0.68*	*0.59*	*0.75*	*0.61*	*0.50*	*0.69*
machair1	dune grassland	1	Scotland, Western Isles	250	0.17	0.14	0.23	0.26	0.22	0.30	0.29	0.24	0.36	0.41	0.36	0.45	0.11	0.08	0.15	0.22	0.19	0.26	0.57	0.51	0.65	0.49	0.41	0.56
					Ø 0.19	**0.16**	**0.22**	**0.25**	**0.23**	**0.30**	**0.30**	**0.26**	**0.35**	**0.40**	**0.36**	**0.45**	**0.12**	**0.08**	**0.15**	**0.19**	**0.16**	**0.22**	**0.56**	**0.52**	**0.62**	**0.50**	**0.44**	**0.56**
evergreen forest																												
BEpine	pine forest, immature timber	400	Germany, Schorfheide-Chorin	11	0.07	0.07	0.09	0.08	0.07	0.09	0.13	0.11	0.15	0.14	0.13	0.16	0.04	0.03	0.05	0.05	0.05	0.07	0.34	0.30	0.35	0.17	0.16	0.21
BEspruce	spruce forest, immature timber	400	Germany, Schwäbische Alb	16	0.15	0.13	0.15	0.18	0.17	0.19	0.25	0.23	0.26	0.30	0.29	0.32	0.10	0.08	0.12	0.13	0.11	0.15	0.52	0.47	0.53	0.38	0.35	0.40
					Ø 0.13	**0.10**	**0.12**	**0.13**	**0.12**	**0.14**	**0.19**	**0.17**	**0.21**	**0.22**	**0.21**	**0.24**	**0.07**	**0.06**	**0.08**	**0.09**	**0.08**	**0.11**	**0.43**	**0.39**	**0.44**	**0.27**	**0.25**	**0.30**
steppe/prairie																												
dat_12	forest steppe	1	Hungary, Kiskunság National Park	100	0.24	0.19	0.28	0.29	0.24	0.33	0.36	0.31	0.42	0.43	0.37	0.48	0.12	0.08	0.17	0.18	0.14	0.21	0.64	0.57	0.71	0.50	0.42	0.61
dat_13	sand prairie	1	USA, Minnesota, Cedar Creek Ecosystem Science Reserve	5	0.31	0.23	0.33	0.30	0.28	0.35	0.45	0.37	0.48	0.44	0.44	0.51	0.20	0.18	0.21	0.24	0.20	0.30	0.74	0.66	0.79	0.51	0.50	0.59
dat_16	sand prairie	0.3	USA, Minnesota, Cedar Creek Ecosystem Science Reserve	23	0.34	0.32	0.37	NA	NA	NA	0.50	0.48	0.52	NA	NA	NA	0.25	0.21	0.28	NA	NA	NA	0.80	0.78	0.83	NA	NA	NA
dat_2	shortgrass prairie	1	USA, Kansas, Hays	15	0.23	0.21	0.24	0.16	0.15	0.17	0.34	0.31	0.36	0.26	0.25	0.27	0.11	0.09	0.14	0.09	0.07	0.11	0.57	0.52	0.59	0.22	0.19	0.26
dat_3	shortgrass prairie	1	USA, Colorado, Nunn, Central Plains Experimental Range	12	0.32	0.28	0.34	0.17	0.13	0.20	0.47	0.43	0.50	0.28	0.21	0.32	0.16	0.10	0.21	0.06	0.04	0.10	0.76	0.73	0.79	0.20	0.08	0.26
dat_4	semi-desert grasslands	1	USA, Arizona, Santa Rita Experimental Range	109	0.23	0.17	0.29	0.26	0.20	0.32	0.35	0.28	0.43	0.39	0.31	0.47	0.08	0.05	0.13	0.09	0.06	0.13	0.60	0.50	0.70	0.40	0.27	0.51
dat_5	sagebrush steppe	1	USA, Idaho	4	0.22	0.20	0.23	0.13	0.12	0.13	0.35	0.32	0.37	0.22	0.22	0.23	0.11	0.10	0.12	0.06	0.05	0.07	0.63	0.59	0.65	0.19	0.18	0.20
dat_66.fall	pinon-juniper woodland	1	USA, New Mexico, Sevilleta National Wildlife Refuge	100	0.39	0.33	0.46	0.35	0.30	0.43	0.55	0.49	0.61	0.50	0.44	0.56	0.19	0.13	0.26	0.20	0.14	0.28	0.84	0.77	0.90	0.51	0.41	0.64
					Ø 0.29	**0.24**	**0.32**	**0.24**	**0.20**	**0.28**	**0.42**	**0.37**	**0.46**	**0.36**	**0.32**	**0.41**	**0.15**	**0.12**	**0.19**	**0.13**	**0.10**	**0.17**	**0.70**	**0.64**	**0.75**	**0.36**	**0.29**	**0.44**
succulent desert vegetation																												
kalaha	Kalahari desert	100	South Africa	20	0.25	0.23	0.28	NA	NA	NA	0.39	0.35	0.42	NA	NA	NA	0.16	0.12	0.18	NA	NA	NA	0.68	0.63	0.72	NA	NA	NA
karoo	Succulent Karoo	100	South Africa	104	0.23	0.21	0.26	NA	NA	NA	0.37	0.34	0.40	NA	NA	NA	0.14	0.11	0.16	NA	NA	NA	0.66	0.62	0.69	NA	NA	NA
					Ø 0.24	**0.22**	**0.27**				**0.38**	**0.34**	**0.41**				**0.15**	**0.12**	**0.17**				**0.67**	**0.62**	**0.71**			
semi-natural temperate grassland																												
BEgrass_chalk	chalk grassland	16	Germany, Schwäbische Alb	13	0.11	0.10	0.12	0.25	0.22	0.26	0.19	0.18	0.22	0.39	0.37	0.41	0.08	0.07	0.09	0.19	0.16	0.20	0.45	0.43	0.48	0.49	0.45	0.55
BEgrass_mesicchalk	mesic chalk grassland	16	Germany, Schwäbische Alb	34	0.13	0.11	0.16	0.26	0.24	0.29	0.23	0.19	0.26	0.41	0.39	0.45	0.10	0.07	0.11	0.21	0.19	0.23	0.50	0.45	0.54	0.52	0.47	0.60
campos025	Brazilian native campos grassland	0.25	Brazil, Eldorado do Sul municipality	15	0.31	0.30	0.34	0.36	0.35	0.40	0.47	0.45	0.50	0.53	0.50	0.56	0.26	0.23	0.29	0.31	0.29	0.34	0.78	0.76	0.81	0.66	0.61	0.70
coastheadlands	Themeda grassland on headlands	4	Australia, East Coast	74	0.22	0.18	0.29	0.21	0.17	0.27	0.35	0.28	0.45	0.34	0.28	0.42	0.14	0.09	0.20	0.15	0.11	0.21	0.64	0.56	0.74	0.35	0.29	0.45
dat_27.1	non serpentine grassland	1	USA, California	205	0.30	0.27	0.34	0.35	0.32	0.39	0.45	0.40	0.49	0.51	0.47	0.56	0.18	0.14	0.22	0.23	0.19	0.27	0.75	0.69	0.79	0.54	0.47	0.60
dat_27.2	serpentine grassland	1	USA, California	195	0.26	0.22	0.30	0.36	0.33	0.41	0.40	0.35	0.45	0.52	0.48	0.57	0.17	0.13	0.21	0.25	0.21	0.29	0.70	0.64	0.75	0.59	0.52	0.67
dat_29	montane *Nardus* grassland	0.25	Czech Republic, Krkonose Mountains	4	0.03	0.01	0.05	NA	NA	NA	0.06	0.03	0.09	NA	NA	NA	0.00	0.00	0.01	NA	NA	NA	0.16	0.08	0.24	NA	NA	NA
dat_30	montane *Nardus* grassland	0.25	Czech Republic, Krkonose Mountains	4	0.08	0.07	0.09	NA	NA	NA	0.14	0.12	0.16	NA	NA	NA	0.05	0.03	0.06	NA	NA	NA	0.37	0.35	0.39	NA	NA	NA

Dataset name	**Vegetation type**	**Plot size (m^2)**	**Location**	**n plots**	**Sørensen index**						**Jaccard index**						**Simpson index**						**Hellinger index**					
					p/a Median	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**	**p/a Median**	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**	**p/a Median**	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**	**p/a Median**	**p/a 25% quantile**	**p/a 75% quantile**	**abund. Median**	**abund. 25% quantile**	**abund. 75% quantile**
dat_39	wet nutrient-poor meadow	0.25	Czech Republic, Ohrazeni	3	0.13	0.12	0.15	NA	NA	NA	0.23	0.22	0.26	NA	NA	NA	0.10	0.08	0.11	NA	NA	NA	0.50	0.48	0.54	NA	NA	NA
dat_70	mesic semi-natural grassland	1	Czech Republic, Zvíkov	10	0.12	0.10	0.14	0.22	0.22	0.24	0.21	0.18	0.24	0.36	0.36	0.38	0.09	0.06	0.11	0.19	0.18	0.21	0.48	0.43	0.51	0.46	0.45	0.48
dat_79	mesic semi-natural grassland	0.25	Estonia, Ahja River	7	0.21	0.19	0.23	0.28	0.26	0.31	0.33	0.31	0.36	0.42	0.41	0.46	0.06	0.04	0.11	0.18	0.15	0.20	0.58	0.56	0.64	0.53	0.47	0.57
devin	dry grassland	16	Czech Republic, Děvín Hill, Pavlov Hills	7	0.20	0.18	0.20	0.26	0.24	0.28	0.33	0.30	0.33	0.40	0.39	0.43	0.13	0.12	0.14	0.19	0.19	0.20	0.62	0.59	0.62	0.56	0.55	0.63
harz	Nutrient-poor mountain meadow	4	Germany, Harz	14	0.07	0.05	0.09	0.08	0.07	0.10	0.13	0.10	0.16	0.15	0.13	0.17	0.04	0.03	0.05	0.06	0.04	0.07	0.36	0.30	0.40	0.20	0.19	0.21
ossekampen	mesic meadow, mown	40	Netherlands, Wageningen	2	0.18	0.18	0.18	0.16	0.16	0.17	0.30	0.30	0.30	0.27	0.27	0.28	0.13	0.13	0.13	0.12	0.12	0.12	0.59	0.59	0.59	0.30	0.29	0.31
xerogr	xerothermic grassland	1	Germany, Halle	3	0.20	0.19	0.20	0.19	0.19	0.21	0.31	0.30	0.32	0.31	0.31	0.33	0.11	0.11	0.11	0.12	0.12	0.13	0.57	0.56	0.59	0.30	0.30	0.32
xerogr_sub	*xerothermic grassland*	*0.01*	*Germany, Halle*	300	*0.33*	*0.26*	*0.43*	*0.39*	*0.31*	*0.48*	*0.42*	*0.34*	*0.50*	*0.50*	*0.42*	*0.57*	*0.22*	*0.13*	*0.33*	*0.26*	*0.17*	*0.37*	*0.58*	*0.48*	*0.67*	*0.51*	*0.40*	*0.60*
					Ø 0.17	**0.15**	**0.19**	**0.25**	**0.23**	**0.28**	**0.27**	**0.25**	**0.30**	**0.39**	**0.36**	**0.42**	**0.11**	**0.09**	**0.13**	**0.18**	**0.16**	**0.21**	**0.54**	**0.50**	**0.57**	**0.46**	**0.42**	**0.51**
mire																												
mire	mire	1	Spain, Navarra	22	0.09	0.05	0.15	0.09	0.05	0.15	0.17	0.09	0.25	0.17	0.09	0.26	0.00	0.00	0.04	0.06	0.03	0.12	0.43	0.30	0.52	0.15	0.09	0.23

Table A16: Model results from logistic models regressing baseline turnover values against the median species richness of the respective plot over the observed years. Models were calculated separately for each dataset, so plots within the same vegetation type and with the same plot sizes are included in one model only. Positive estimates are coloured green, negative estimates are coloured red. *P*-values were corrected for multiple testing with the "false discovery rate" method of the function "p-adjust".

Dataset	**Sørensen p/a**		**Sørensen abundance**		**Jaccard p/a**		**Jaccard abundance**		**Simpson p/a**		**Simpson abundance**		**Hellinger p/a**		**Hellinger abundance**	
	estimate	**p**	***estimate***	***p***	***estimate***	***p***	***estimate***	***p***	***estimate***	***p***	***estimate***	***p***	**estimate**	***p***	**estimate**	***p***
aelmoeseneiebos	0.13	1	0.2	1	0.19	1	0.21	1	0.52	1	0.27	1	0.78	1	2.64	1
alpinegr	0	1	−0.08	1	0.01	1	−0.07	1	1.49	1	−0.01	1	0.54	1	−0.57	1
BEdeci	−0.03	1	−0.02	1	−0.02	1	−0.01	1	−0.03	1	−0.02	1	−0.01	1	−0.02	1
BEgrass_chalk	−0.02	1	0	1	−0.02	1	0	1	−0.05	1	−0.01	1	−0.08	1	0.1	1
BEgrass_mesicchalk	0.01	1	0.01	1	0.01	1	0.01	1	0.01	1	0.01	1	0.03	1	0.03	1
BEpine	0.01	1	0.01	1	0.01	1	0.01	1	0.02	1	0.03	1	0.06	1	0.07	1
BEspruce	−0.01	1	−0.01	1	−0.01	1	−0.01	1	−0.02	1	−0.02	1	−0.04	1	−0.01	1
coastheadlands	0.03	1	0.04	1	0.03	1	0.04	1	0.04	1	0.07	1	0.05	1	0.1	1
coolibah	−0.01	1	−0.01	1	0.01	1	0.01	1	0	1	0.01	1	0.02	1	0.02	1
dat_12	−0.05	1	−0.06	1	−0.03	1	−0.04	1	−0.04	1	−0.04	1	−0.01	1	−0.01	1
dat_13	−0.17	1	0	1	−0.17	1	0	1	−0.11	1	−0.1	1	−1.12	1	0.05	1
dat_16	0.02	1	.	.	0.03	1	.	.	0.07	1	.	.	0.21	1	.	.
dat_2	0.08	1	0.06	1	0.09	1	0.06	1	0.13	1	0.02	1	0.37	1	0.23	1
dat_27.1	0.01	1	0.03	1	0.01	1	0.03	1	0.02	1	0.03	1	0.03	1	0.08	1
dat_27.2	−0.01	1	0.01	1	0	1	0.01	1	0.01	1	0.02	1	0	1	0.05	1
dat_28	0.47	1	0.42	1	0.62	1	0.55	1	0.19	1	0.34	1	1.06	0.82	0.85	1
dat_29	0.2	1	.	.	0.21	1	.	.	1.64	1	.	.	0.56	1	.	.
dat_3	0.1	1	0.1	1	0.11	1	0.1	1	0.22	1	0.33	1	0.57	1	0.37	1
dat_30	0	1	.	.	0	1	.	.	−0.05	1	.	.	0.17	1	.	.
dat_31	0.07	1	0.05	1	0.08	1	0.06	1	0.12	1	0.11	1	0.31	1	0.3	1
dat_39	−0.1	1	.	.	−0.1	1	.	.	−0.06	1	.	.	−0.9	1	.	.
dat_4	−0.03	1	−0.03	1	−0.01	1	0	1	0.02	1	−0.02	1	0.06	1	0.15	1
dat_5	−0.13	1	0.08	1	−0.14	1	0.08	1	−0.09	1	0.03	1	−1.45	1	1.68	1
dat_53.creo	0.07	1	−0.02	1	0.11	1	0.02	1	−0.04	1	−0.06	1	0.33	0.16	0.12	1
dat_53.grama	0.05	1	0.16	1	0.07	1	0.17	1	0.1	1	0.17	1	0.19	1	0.34	0.2

Dataset	**Sørensen p/a**		**Sørensen abundance**		**Jaccard p/a**		**Jaccard abundance**		**Simpson p/a**		**Simpson abundance**		**Hellinger p/a**		**Hellinger abundance**	
	estimate	**p**	***estimate***	***p***	***estimate***	***p***	***estimate***	***p***	***estimate***	***p***	***estimate***	***p***	**estimate**	***p***	**estimate**	***p***
dat_53.mesq	0	1	0.01	1	0.07	1	0.06	1	−0.1	1	−0.09	1	0.41	0.16	0.27	0.82
dat_53.playa	0.1	1	0.22	1	0.16	1	0.26	1	0.2	1	0.25	1	0.65	0.39	0.79	0.16
dat_53.tarb	−0.18	1	−0.24	1	−0.1	1	−0.18	1	−0.41	1	−0.45	1	0.16	1	−0.03	1
dat_65.fall	0.07	1	0.13	1	0.12	1	0.15	1	0.15	1	0.19	1	0.36	1	0.4	1
dat_66.fall	0.04	1	0.06	1	0.06	1	0.07	1	0.11	1	0.1	1	0.18	1	0.16	1
dat_67.4	−0.11	1	0.04	1	−0.1	1	0.04	1	−0.1	1	0.02	1	−0.58	1	0.45	1
dat_67.5	−0.04	1	−0.05	1	−0.03	1	−0.04	1	0.02	1	−0.02	1	−0.31	1	0.33	1
dat_67.grama	−0.04	1	0.09	1	−0.04	1	0.08	1	−0.06	1	0.08	1	−0.37	1	0.56	1
dat_7.1	−0.14	1	−0.27	0.82	−0.08	1	−0.22	1	−0.18	1	−0.24	1	0.03	1	−0.15	1
dat_7.2	0.07	1	0.16	1	0.08	1	0.16	1	0.09	1	0.17	1	0.19	1	0.32	0.51
dat_70	0	1	0.03	1	0	1	0.03	1	0.03	1	0.06	1	0	1	0.25	1
dat_77	0.01	1	0.07	1	0.01	1	0.07	1	0.06	1	0.11	1	0.05	1	0.34	1
dat_79	0	1	0.01	1	0	1	0.01	1	0.04	1	0.04	1	−0.17	1	−0.02	1
devin	0.04	1	0.01	1	0.04	1	0.01	1	0.05	1	0.01	1	0.4	1	−0.18	1
expmachair	0	1	−0.02	1	0.01	1	−0.01	1	0.06	1	−0.02	1	0.08	1	−0.1	1
campos025	0.02	1	0.03	1	0.02	1	0.03	1	0.03	1	0.02	1	0.11	1	0.22	1
hardwood	−0.09	1	−0.15	1	−0.08	1	−0.13	1	−0.26	1	−0.15	1	−0.25	1	−0.51	1
goe_cont	0.02	1	0	1	0.02	1	0.01	1	−0.02	1	0.03	1	0.18	1	0.57	1
goe_subplots	−0.24	1	0.05	1	−0.25	1	0.05	1	−0.26	1	−0.05	1	−0.76	1	0.61	1
harz	−0.06	1	−0.02	1	−0.05	1	−0.02	1	−0.05	1	−0.04	1	−0.14	1	−0.01	1
kalaha	−0.01	1	.	.	−0.01	1	.	.	0.02	1	.	.	0.02	1	.	.
karoo	0	1	.	.	0	1	.	.	0.01	1	.	.	0	1	.	.
machair004	−0.02	1	−0.03	1	−0.03	1	−0.03	1	0.02	1	−0.04	1	−0.09	1	−0.06	1
machair02	−0.05	1	−0.05	1	−0.05	1	−0.04	1	−0.03	1	−0.05	1	−0.06	1	−0.06	1
machair1	−0.02	1	0	1	−0.01	1	0	1	−0.01	1	0	1	−0.01	1	0.02	1
xero_sub	−0.36	1	−0.35	1	−0.2	1	−0.22	1	−0.74	1	−0.61	1	0.49	1	0.65	1
mire	−0.07	1	0.03	1	−0.05	1	0.03	1	0.09	1	0.02	1	−0.03	1	0.04	1
desertgr	−0.07	1	0.02	1	−0.06	1	0.02	1	−0.04	1	0.04	1	−0.26	1	0.21	1
ossekampen	−0.01	1	0.03	1	0	1	0.03	1	0.02	1	0.02	1	−10.47	1	10.47	1
snowbed	−0.31	1	.	.	−0.29	1	.	.	−0.25	1	.	.	−0.88	1	.	.
stenshuvud	−0.02	1	−0.02	1	−0.01	1	−0.01	1	0.06	1	0	1	0.08	1	0.06	1

Table A17: Model results from logistic models regressing baseline turnover values against the mean share of annual species in the respective plot over the observed years. Models were calculated separately for each dataset, so plots within the same vegetation type and with the same plot sizes are included in one model only. Positive estimates are coloured green, negative estimates are coloured red. *P*-values were corrected for multiple testing with the "false discovery rate" method of the function "p-adjust".

Dataset	**Sørensen p/a**		**Sørensen abundance**		**Jaccard p/a**		**Jaccard abundance**		**Simpson p/a**		**Simpson abundance**		**Hellinger p/a**		**Hellinger abundance**	
	estimate	***p***	**estimate**	***p***	**estimate**	***p***	**estimate**	***p***	**estimate**	***p***	**estimate**	***p***	**estimate**	***p***	**estimate**	***p***
alpinegr	5.29	1	−111.78	1	5.9	1	−123.26	1	32.47	1	−488.76	1	47.73	1	−736.14	1
BEdeciduous	−1.3	1	−0.33	1	−0.63	1	−0.21	1	−2.45	1	−0.48	1	0.09	1	0.25	1
BEgrass_chalk	2.53	1	2.25	1	2.46	1	2.38	1	3.96	1	3.96	1	9.32	1	13.06	1
BEgrass_mesicchalk	1.88	1	−1.04	1	1.94	1	−1.05	1	2.04	1	−0.36	1	5.85	1	−2.11	1
BEpine	1.16	1	24.51	1	1.12	1	23.7	1	−2.27	1	27.4	1	3.04	1	94.25	1
BEspruce	−2.59	1	0.82	1	−1.76	1	0.51	1	−10.3	1	2	1	4.67	1	1	1
coastheadlands	1.9	1	1.26	1	1.97	1	1.87	1	2.43	1	4.67	1	3.11	1	−1.84	1
coolibah	0.72	1	−1.09	1	1	1	−1.16	1	2.9	1	1.6	1	1.56	1	0.45	1
devin	3.54	1	1.76	1	3.71	1	1.79	1	5.17	1	1.53	1	42.36	1	78.73	1
expmachair	−3.13	1	−10.86	1	−2.19	1	−7.72	1	2.83	1	−12.95	1	−2.32	1	−45.37	1
campos025	3.11	1	7.12	1	3.37	1	4.32	1	0.17	1	0.81	1	19.08	1	64.03	1
goe_subplots	−1.26	1	400.28	1	−1.7	1	406.21	1	4.01	1	237.36	1	−5.5	1	4363.9	1
harz	11.23	1	14.29	1	11.21	1	12.42	1	10.59	1	20.08	1	39.16	1	19.95	1
kalaha	1.2	1	.	.	1.03	1	.	.	2.25	1	.	.	2.44	1	.	.
karoo	1.39	1	.	.	1.33	1	.	.	1.25	1	.	.	3.2	1	.	.
machair004	−1.93	1	0.34	1	−1.53	1	0.67	1	−2.14	1	1.49	1	−1.59	1	1.49	1
machair02	−1.18	1	0.88	1	−1.03	1	0.86	1	−2.22	1	0.76	1	−1.51	1	1.06	1
machair1	3.43	1	1.67	1	3.19	1	1.53	1	4.64	1	0.25	1	4.48	1	2.63	1
xerogr	6.58	1	23.86	1	12.89	1	24.78	1	−15.37	1	22.71	1	825.17	1	11 259.79	1
xerogr_sub	0.36	1	0.55	1	0.3	1	0.15	1	0.42	1	0.89	1	0.76	1	1.35	1
mire	−1.24	1	−0.89	1	0.96	1	−0.68	1	7.12	1	−1.17	1	0.44	1	−2.16	1
desertgr	1.53	1	2.01	1	1.43	1	1.96	1	2.02	1	2.05	1	6.86	1	10.74	1
snowbed	2.88	1	.	.	2.47	1	.	.	−7.47	1	.	.	4.76	1	.	.

Table A18: Model estimates of multiple mixed logistic models for the seven predictor variables (columns) and the response variable baseline turnover, expressed as eight different dissimilarity indices (rows), respectively. Minimal adequate models were chosen after ranking all possible predictor combinations by the Akaike information criterion (AIC). For each response variable, the top model with the lowest AIC and those with ΔAIC < 2 are reported. Two sets of multiple models were constructed. The first set included the proportion of annual species as well as species saturation as predictors and the other excluded them, since these variables were only available for approximately half of the sampled plots (see Table 5.1). "n.a." denotes that the respective predictor was not part of the full model. Dataset was used as a random factor.

	Intercept	**Saturation**	**Plot size**	**% Annual species**	**Mean temperature**	**Species richness**	**Seasonality Rainfall**	**Annual rainfall**	**AIC**
Model set 1 (n = 1622 p/a-based, n = 1488 abundance-based)									
Sørensen p/a	−1.00	−0.27	-0.25	0.14	0.16	.	.	.	119.52
	−1.06	−0.33	-0.21	0.18	.	.	.	.	120.58
	−1.15	−0.28	-0.26	0.17	0.19	.	−0.18	.	120.68
	−0.97	−0.26	-0.22	.	0.21	.	.	.	121.16
	−0.99	−0.26	-0.26	0.13	0.16	.	.	-0.03	121.45
	−1.01	−0.28	-0.26	0.14	0.16	0.02	.	.	121.49
Sørensen abundance	−0.87	−0.35	-0.31	0.18	.	0.15	.	.	108.91
	−0.82	−0.32	-0.34	0.15	0.13	0.17	.	.	108.98
	−0.81	−0.27	-0.22	0.17	.	.	.	.	109.14
	−0.76	−0.23	-0.23	0.14	0.12	.	.	.	109.67
	−0.76	−0.31	-0.35	0.12	0.15	0.18	.	-0.09	110.51
	−0.66	−0.31	-0.34	.	0.22	0.18	.	-0.20	110.65
	−0.80	−0.35	-0.31	0.17	.	0.15	0.08	.	110.82
	−0.85	−0.35	-0.31	0.17	.	0.15	.	-0.03	110.84
Jaccard p/a	−0.40	−0.24	-0.20	0.17	0.21	.	.	.	121.13
	−0.42	−0.28	-0.24	0.17	0.22	0.07	.	.	122.57
	−0.38	−0.24	-0.20	0.17	0.21	.	.	-0.02	123.10
	−0.43	−0.24	-0.20	0.18	0.21	.	−0.03	.	123.11
Jaccard abundance	−0.25	−0.27	-0.33	0.14	0.15	0.18	.	.	108.38
	−0.31	−0.31	-0.30	0.18	.	0.16	.	.	109.01
	−0.20	−0.27	-0.29	.	0.22	0.17	.	.	110.00
	−0.19	−0.18	-0.21	0.13	0.14	.	.	.	110.10
	−0.25	−0.22	-0.19	0.16	.	.	.	.	110.20
	−0.22	−0.27	-0.33	0.13	0.16	0.18	.	-0.04	110.27
	−0.17	−0.27	-0.32	0.13	0.14	0.18	0.09	.	110.28
Simpson p/a	−1.54	−0.28	-0.25	0.15	0.16	.	.	.	153.45
	−1.60	−0.34	-0.20	0.19	.	.	.	.	153.70

	Intercept	**Saturation**	**Plot size**	**% Annual species**	**Mean temperature**	**Species richness**	**Seasonality Rainfall**	**Annual rainfall**	**AIC**
	−1.75	−0.30	-0.27	0.20	0.20	.	−0.26	.	154.01
	−1.51	−0.28	-0.21	.	0.21	.	.	.	154.89
	−1.57	−0.32	-0.30	0.16	0.17	0.08	.	.	155.05
	−1.55	−0.29	-0.25	0.16	0.15	.	.	0.01	155.44
Simpson abundance	−1.28	−0.38	-0.33	0.17	.	0.20	.	.	129.39
	−1.24	−0.36	-0.36	0.15	0.12	0.23	.	.	129.97
	−1.37	−0.39	-0.33	0.22	.	0.20	.	0.15	130.26
	−1.20	−0.27	-0.20	0.16	.	.	.	.	130.58
	−1.31	−0.38	-0.33	0.18	.	0.20	−0.02	.	131.38
	−0.12	−0.12	-0.10	0.16	0.19	.	.	.	99.12
Hellinger p/a	−0.16	−0.13	.	0.15	0.17	.	.	.	99.22
	−0.12	.	-0.12	0.16	0.24	.	.	.	99.39
	−0.24	−0.15	.	0.19	0.15	.	.	0.14	99.81
	−0.18	.	.	0.13	0.24	.	.	.	100.04
	−0.20	−0.13	-0.09	0.20	0.16	.	.	0.12	100.10
	0.22	.	.	.	0.21	.	0.38	.	100.15
	−0.14	−0.12	.	.	0.23	.	.	.	100.47
	−0.32	−0.20	.	0.23	.	.	.	0.17	100.48
	−0.14	−0.15	-0.14	0.16	0.19	0.06	.	.	100.68
	−0.23	−0.18	.	0.19	.	.	.	.	100.72
	0.16	−0.10	.	.	0.18	.	0.31	.	100.72
	−0.16	.	.	.	0.28	.	.	.	100.73
	−0.13	.	.	0.15	0.22	-0.07	.	.	100.74
	−0.17	.	-0.11	0.18	0.23	.	.	0.08	100.93
	−0.02	−0.12	.	0.12	0.16	.	0.14	.	100.95
	−0.14	−0.11	.	0.15	0.17	-0.03	.	.	101.04
	−0.11	.	-0.10	.	0.29	.	.	.	101.08
	0.08	.	.	0.09	0.21	.	0.26	.	101.08
	0.20	.	-0.08	.	0.23	.	0.33	.	101.11
	−0.10	−0.11	-0.10	0.16	0.18	.	0.02	.	101.11
Hellinger abundance	−0.53	.	-0.16	0.15	0.21	.	.	.	134.05
	−0.56	−0.17	-0.26	0.15	0.17	0.17	.	.	134.33
	−0.10	.	.	.	0.20	.	0.47	.	134.48
	−0.62	.	.	0.12	0.22	.	.	.	134.65
	−0.57	.	.	.	0.27	.	.	.	134.93
	−0.64	−0.21	-0.24	0.18	.	0.15	.	.	135.03
	−0.51	−0.08	-0.15	0.15	0.17	.	.	.	135.06
	0.00	.	.	.	.	.	0.65	.	135.14
	−0.25	.	.	0.09	0.17	.	0.35	.	135.35
	−0.59	−0.13	-0.13	0.18	.	.	.	.	135.37
	−0.55	.	-0.22	0.15	0.23	0.07	.	.	135.39

	Intercept	**Saturation**	**Plot size**	**% Annual species**	**Mean temperature**	**Species richness**	**Seasonality Rainfall**	**Annual rainfall**	**AIC**
	−0.19	.	.	0.10	.	.	0.49	.	135.48
	−0.59	−0.09	.	0.12	0.17	.	.	.	135.49
	−0.31	.	-0.14	0.12	0.18	.	0.22	.	135.52
	−0.65	−0.14	.	0.15	.	.	.	.	135.53
	−0.10	.	-0.10	.	0.21	.	0.41	.	135.60
	−0.50	.	-0.12	.	0.28	.	.	.	135.60
	−0.54	−0.09	.	.	0.22	.	.	.	135.82
	−0.07	−0.10	.	.	.	.	0.53	.	135.86
	−0.14	−0.07	.	.	0.17	.	0.41	.	135.91
	−0.40	−0.17	-0.25	0.13	0.16	0.17	0.16	.	136.01
	−0.55	.	-0.16	0.15	0.20	.	.	0.03	136.02
	−0.27	−0.10	.	0.11	.	.	0.36	.	136.02
	−0.65	.	-0.15	0.19	.	.	.	.	136.04
Model set 2 (n = 3558 p/a-based, n = 3390 abundance-based)									
Sørensen p/a	−0.80	n.a.	-0.27	n.a.	0.23	.	0.11	-0.20	267.02
	−0.81	n.a.	-0.29	n.a.	0.28	.	.	-0.24	267.18
	−0.81	n.a.	-0.21	n.a.	0.25	-0.11	.	-0.20	267.35
	−0.80	n.a.	-0.21	n.a.	0.21	-0.09	0.10	-0.17	267.79
Sørensen abundance	−0.63	n.a.	-0.22	n.a.	0.18	.	0.12	-0.11	293.64
	−0.63	n.a.	-0.21	n.a.	0.20	.	0.16	.	293.70
	−0.64	n.a.	-0.24	n.a.	0.23	.	.	-0.15	294.05
	−0.63	n.a.	-0.25	n.a.	0.19	0.04	0.12	-0.12	295.44
Jaccard p/a	−0.26	n.a.	-0.22	n.a.	0.22	.	0.15	-0.14	281.56
	−0.25	n.a.	-0.20	n.a.	0.24	.	0.20	.	283.01
	−0.26	n.a.	-0.20	n.a.	0.21	-0.03	0.14	-0.13	283.33
	−0.27	n.a.	-0.25	n.a.	0.28	.	.	-0.19	283.36
Jaccard abundance	−0.07	n.a.	-0.18	n.a.	0.17	.	0.16	.	279.69
	−0.07	n.a.	-0.22	n.a.	0.19	0.05	0.18	.	281.08
	−0.08	n.a.	-0.19	n.a.	0.16	.	0.15	-0.05	281.18
Simpson p/a	−1.47	n.a.	-0.24	n.a.	0.25	.	.	-0.13	379.30
	−1.46	n.a.	-0.22	n.a.	0.29	.	.	.	379.89
	−1.47	n.a.	-0.15	n.a.	0.25	-0.10	.	.	380.58
	−1.46	n.a.	-0.21	n.a.	0.24	.	0.09	.	380.73
	−1.50	n.a.	.	n.a.	0.20	-0.18	.	.	380.90
	−1.47	n.a.	-0.20	n.a.	0.23	-0.06	.	-0.11	380.93
	−1.47	n.a.	-0.23	n.a.	0.23	.	0.05	-0.12	380.99
Simpson abundance	−1.26	n.a.	-0.18	n.a.	0.17	.	.	.	350.44
	−1.25	n.a.	-0.22	n.a.	0.19	0.05	.	.	352.11
	−1.25	n.a.	-0.18	n.a.	0.18	.	.	0.03	352.35
	−1.26	n.a.	-0.18	n.a.	0.17	.	0.01	.	352.43
	−0.03	n.a.	-0.09	n.a.	0.16	.	0.15	.	222.72

Hellinger	**Intercept**	**Saturation**	**Plot size**	**% Annual species**	**Mean temperature**	**Species richness**	**Seasonality Rainfall**	**Annual rainfall**	**AIC**
p/a	−0.05	n.a.	.	n.a.	0.14	.	0.16	.	223.30
	−0.03	n.a.	-0.10	n.a.	0.15	.	0.14	-0.02	224.58
	−0.03	n.a.	-0.10	n.a.	0.16	0.02	0.15	.	224.63
Hellinger abundance	−0.52	n.a.	-0.21	n.a.	0.23	0.12	.	.	325.85
	−0.51	n.a.	-0.21	n.a.	0.20	0.14	0.09	.	326.63
	−0.52	n.a.	-0.11	n.a.	0.18	.	.	.	326.73
	−0.56	n.a.	.	n.a.	0.18	.	.	.	326.76
	−0.52	n.a.	-0.22	n.a.	0.23	0.13	.	-0.03	327.72

7.5 References

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