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Impacts of nitrogen and sulphur depositions alongside climate warming on Austrian grassland communities using data from the last 100 years

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Abstract

Nitrogen and sulphur depositions as well as rising temperatures represent changes in key drivers of plant species composition brought about through both natural and anthropogenic activities. Industrialisation and agricultural intensification have caused changes in nitrogen and sulphur emissions both historically and presently, exacerbating effects linked to climate change, such as biodiversity and habitat loss. Here, we leveraged spatio-temporal data of these drivers alongside vegetation survey data of select Austrian vegetation types, stretching back almost a century, to study their relationships using predictive random forest models. With a focus on nutrient-poor grassland communities, predictions were made for alpha biodiversity (species number per plot) and various ecological indicator metrics (nutrients, temperature, reaction, moisture) on the basis of anomalies in nitrogen deposition, sulphur deposition, and temperature relative to pre-industrial baselines.

The degree of the increase in nitrogen deposition had a slight positive effect on alpha biodiversity in most communities and was associated with a shift towards a more nitrophilic species profile. The degree of the increase in sulphur depositions, on the other hand, showed minimal effect on alpha biodiversity, potentially due to confounding effects from other variables. Unexpectedly, both nitrogen and sulphur depositions correlated with a shift towards a more basophilic species profile; it is speculated that correlations between variables, namely temperature, underpin this result. The effect of increased temperature on alpha biodiversity was found to vary strongly across communities, with effects of increased drying thought to play a prominent role. Increased temperature further correlated weakly with a shift toward a more thermophilic species profile, with stronger effects observed in alpine and subalpine vegetation classes, while the correlation between temperature increases and moisture indicators was largely negligible. These results shed not only light on the effects of chemical depositions on different grassland communities — a relatively unexplored area of research, but also provide insight on which specific communities may be more at risk by chemical depositions and climate warming.

Keywords: nitrogen deposition, sulphur deposition, temperature increase, grassland communities, alpha biodiversity, community composition

Kurzfassung

Stickstoff- und Schwefeldepositionen sowie steigende Temperaturen stellen Veränderungen der wichtigsten Einflussfaktoren für die Artenzusammensetzung von Pflanzengemeinschaften dar. Industrialisierung und landwirtschaftliche Intensivierung haben in der Vergangenheit sowie in der Gegenwart zu Veränderungen der Stickstoff- und Schwefelemissionen geführt und damit die mit dem Klimawandel verbundenen Auswirkungen, wie den Biodiversitäts- und Lebensraumverlust, verschärft. In meiner Arbeit habe ich räumlich-zeitliche Daten dieser Einflussfaktoren zusammen mit Vegetationserhebungsdaten bestimmter österreichischer Vegetationstypen aus dem letzten Jahrhundert genutzt, um Zusammenhänge mit Hilfe von prädiktiven Random-Forest-Modellen zu untersuchen. Mit Schwerpunkt auf nährstoffarmen Graslandgemeinschaften wurden Vorhersagen für die Alpha-Diversität (Artenzahl pro Flächeneinheit) und verschiedene ökologische Indikatorparameter (Nährstoffe, Temperatur, Reaktion, Feuchtigkeit) auf der Grundlage von Anomalien bei der Stickstoff- und Schwefeldeposition sowie der Temperatur im Vergleich zu vorindustriellen Basiswerten getroffen.

Der Anstieg der Stickstoffdepositionen hatte in den meisten Gemeinschaften einen leicht positiven Effekt auf die Alpha-Diversität und war mit einer Verschiebung hin zu einem nitrophileren Artenprofil verbunden. Der Anstieg der Schwefeldepositionen hingegen zeigte nur minimale Auswirkungen auf die Alpha-Diversität, was möglicherweise auf Störeffekte durch andere Variablen zurückzuführen ist. Überraschenderweise korrelierten sowohl Stickstoff- als auch Schwefeldepositionen mit einer Verschiebung hin zu einem basophileren Artenprofil; vermutlich ist dieses Ergebnis auf Korrelationen zwischen Variablen, insbesondere der Temperatur, zurückzuführen. Der Einfluss erhöhter Temperaturen auf die Alpha-Diversität variierte stark zwischen den Gemeinschaften, wobei Auswirkungen erhöhter Trockenheit vermutlich eine wichtige Rolle spielten. Darüber hinaus korrelierte der Temperaturanstieg schwach mit einer Verschiebung hin zu einem thermophileren Artenprofil, wobei stärkere Effekte in alpinen und subalpinen Vegetationsklassen beobachtet wurden; dabei war die Korrelation zwischen Temperaturanstieg und Feuchtigkeitsindikatoren weitgehend vernachlässigbar. Diese Ergebnisse geben nicht nur Aufschluss über die Auswirkungen chemischer Depositionen auf verschiedene Graslandgemeinschaften — ein relativ unerforschtes Forschungsgebiet, sondern liefern auch Erkenntnisse darüber, welche spezifischen Gemeinschaften durch chemische Depositionen und die Klimaerwärmung stärker gefährdet sein könnten.

Schlagwörter: Stickstoffdeposition, Schwefeldeposition, Temperaturanstieg, Graslandgemeinschaften, Alpha-Diversität, Artenzusammensetzung.

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1. Introduction

1.1 Nitrogen deposition

Airborne nitrogen (N) emissions resulting from various human activities ranging from agriculture to the burning of fossil fuels are known to pose a threat to plant biodiversity in parts of Europe as well as North America (Bobbink *et al.*, 2010; Dise *et al.*, 2011; Simkin *et al.*, 2016; Payne *et al.*, 2017; Staude *et al.*, 2022). Nitrogen deposition describes the introduction of reactive N species from the atmosphere to the biosphere either through precipitation (wet deposition) or in the form of particles or gas (dry deposition) leading to an accumulation of N species in the ecosystem over time (Aber *et al.*, 1998; Matson *et al.*, 2002). Nitrogen deposition occurs in two forms: oxidised N, namely nitrogen oxides (NO_x) such as nitrate (NO_3^-), which are produced primarily through the combustion of fossil fuels; reduced N (NH_x), namely ammonium (NH_4^+) as a byproduct of agricultural ammonia (NH_3) from fertiliser and husbandry (Dignon & Hameed, 1989).

The impacts of increased N levels on changes in plant abundance and composition depend on various ecological factors such as the nutrient status of the soil, the species present and their interactions with one another, and the degree of N deposition in its various forms. As plant growth is often limited by the amount of available N, N depositions at lower levels are associated with increased rates of plant productivity. Higher levels of N concentrations in the atmosphere and N deposition, however, are associated with harmful direct and indirect effects on ecosystems such as acidification of soil and water, toxicity to plant species at higher N concentrations, eutrophication, and changes to the susceptibility of plant species to stressors (Bobbink *et al.*, 2022).

Many studies conducted in European grassland habitats have indeed found a negative correlation between N input (through N deposition or fertiliser or both) and plant species number (Duprè *et al.*, 2010; Stevens *et al.*, 2010a; Wesche *et al.*, 2012; Roth *et al.*, 2013, 2015; Storkey *et al.*, 2015). There is, however, a dearth of comparable research on Austrian grasslands, with related studies conducted in Switzerland often acting as a comparison despite the Switzerland generally showing high N depositions across relatively larger areas of the country compared to Austria (EMEP, 2024). A study by Roth *et al.* (2015) conducted on predominantly calcareous soils of various habitat types in Switzerland predicted a 3–5% decrease in species richness in relation to N deposition, whilst a study by Stevens *et al.* (2010a) conducted on acidic grasslands in Western Europe found a curvilinear negative relationship between N deposition and species richness, such that the former had more strongly negative effects on the latter when background N levels were low. Results from the Park Grass Experiment at Rothamsted Research found that more base-poor plots experienced larger reductions in species richness due to N deposition, with the authors arguing that this was due to the combined eutrophying and acidifying effects of N being more pronounced on more acidic

soils (Storkey *et al.*, 2015). Taken together, these findings suggest that substrate pH plays an important role, with base-rich substrates being less sensitive to N depositions than base-poor ones (Diekmann *et al.*, 2014). There is, however, also some evidence of N deposition promoting species richness, as in the study of grazed subalpine grasslands in the Pyrenees by Boutin *et al.* (2010). These authors found that tracheophyte species richness increased in response to increased temperature and N deposition coupled with long-term grazing, which the authors propose may constitute a release from abiotic constraints that would otherwise reduce species richness. Lastly, there is also evidence for dosage and duration of N input being additive in their negative effect on species richness (Humbert *et al.*, 2016), painting an increasingly complex picture of the relationship between N deposition and species richness.

Increases in available N in ecosystems are furthermore associated with changes to plant community composition: through a proliferation of fast-growing species able to mobilise N more effectively, species less able to mobilise N, often adapted to nutrient-poor conditions, are outcompeted (Hautier *et al.*, 2009; Farrer & Suding, 2016). Certain ecosystems, namely oligotrophic and mesotrophic habitats, are more sensitive to disruption through N inputs, as their native species tend to be adapted to nutrient-poor conditions (Bobbink *et al.*, 2022). Various studies of European grassland communities have linked shifts towards more nitrophilic/nutrophilic communities to higher N levels (e.g. Wesche *et al.*, 2012; Klinkovská *et al.*, 2024; Rumpf *et al.*, 2025), though Roth *et al.* (2019) found no significant change in the nutrophilic values of their surveyed Swiss mountain hay meadows between 2003–2017, suggesting longer timeframes may be required for effects of N deposition on community composition to become visible. Additionally, N deposition has been shown to be linked to decreases in soil pH and a corresponding shift towards more acid-tolerant and acidophilic communities (Stevens *et al.*, 2010a, 2010b), though evidence to the contrary suggests there may be more complex interactions governing N deposition, soil pH, and community acid-/ and base-tolerance (Häberlin & Dengler, 2025; Rumpf *et al.*, 2025).

Thus, over sufficiently long periods of time, high N deposition can lead to altered community structures, with certain species being driven to local extinction while others are novel colonisers (Bobbink *et al.*, 2010). This turn-over is often associated with a shift from small- to large-range species (Staude *et al.*, 2022) and does not necessarily result in a decrease of species richness, as immigration of colonisers and extinction of native species may balance out (Hillebrand *et al.*, 2018). Although research from Swiss mountain grasslands has suggested that N deposition-induced decreases in oligotrophic species outweigh increases in eutrophic species (Roth *et al.*, 2013), the aforementioned study by Roth *et al.* (2015) found that amongst a number of plant diversity metrics it was species richness that had the weakest negative relation to N deposition (3–5%), while phylogenetic diversity had the strongest (11–19%), highlighting the importance of employing different community composition metrics when studying the effects of N inputs on ecosystems.

Long-term damage is done to ecosystems when the accumulation of N surpasses its critical load, which can be estimated for individual ecosystems and can be used to inform decisions around prescribed legal limits of specific pollutants and conservation efforts (Nilsson, 1988; Bobbink *et al.*, 2022). The critical load of N deposition may also vary depending on the habitat type, with Roth *et al.* (2013) finding the expert-set upper limit of 20 kg N ha^{-1} a^{-1} for Swiss mountain hay meadows to be too high, and N deposition already having negative effects on species richness and diversity at 10–15 kg N ha^{-1} a^{-1}. Evidence from acidic grasslands also suggests that N input at low background N levels reduces species richness even when the suggested critical load is not exceeded (Stevens *et al.*, 2010a).

According to the latest EMEP report (2024), N deposition has hotspots in the Netherlands, northern Germany, Belgium, and Poland, which were also found to exceed their critical loads for acidification due to N and S. In total 61% of ecosystem area across Europe was found to exceed its critical load for eutrophication in 2022, highlighting the scope of the threat to native biodiversity. In Austria, there is considerable spatial variation of N deposition, with the highest values in the Northern and South-Eastern Alpine foothills, whilst the depositions in the Central and Southern Alps are relatively low (Buxbaum *et al.*, 2023). Accordingly, high critical load exceedances occur in the former areas (Dirnböck *et al.*, 2017).

The deposition of N in Europe increased in the first half of the 20th century, especially following the Second World War as industrialisation mounted, reached its peak in the 1980s, after which it declined again reflecting efforts to reduce pollution and development of cleaner technology (Engardt *et al.*, 2017; EMEP, 2023). Nitrogen is retained in the soil for at least several years, depending on a number of factors, with ammonia, for instance, being highly immobile in the soil with relatively low rates of leaching (Power *et al.*, 1998; Nielsen *et al.*, 2000). With nitrate fertiliser having an estimated 30 years mean residence time in the soil, a 3-decade accumulation window can be employed when investigating the effect of N deposition on an ecosystem (Sebilo *et al.*, 2013; Rowe *et al.*, 2017). Roth *et al.* (2019) summarises why N depositions may continue to negatively affect plant communities in the present despite generally decreasing for decades, for instance due to limited dispersal of oligotrophic species (Dirnböck & Dullinger, 2004) or through communities reaching stable states with coloniser species remaining despite lowered N deposition (Stevens, 2016). Given the high proportion of vegetation in Europe exceeding its N critical load, the long-term retention of N in ecosystems, and its ongoing effects on plant communities, historical data going back many decades should be used not only to monitor N depositions, but also to analyse its effects on ecosystems through the use of long-term vegetation survey data.

1.2 Sulphur deposition

Sulphur (S) deposition, analogous to that of nitrogen, describes the introduction of reactive S species, typically in the form of oxidised S (SO_x), from the atmosphere to the biosphere, accumulating in the ecosystem over time (Greaver *et al.*, 2012). The predominant species of S is SO_2, emitted through the combustion of fossil fuels, smelting of sulphide ores, as well as by natural activities like volcanic eruptions (Gao *et al.*, 2018). Being a macronutrient for plants, adequate S concentrations are essential for proper plant growth and development as well as ecosystem productivity, however excessive S can incur negative ecological consequences. Primary amongst these is the acidification of soil and water (Varshney *et al.*, 1979). An ecosystem's sensitivity to acid deposition depends on a number of factors, including vegetation, surface geology and topology, and water flow and drainage (Lawrence *et al.*, 1999; Greaver *et al.*, 2012). Research focusing on the effects of S deposition on European grasslands is far less extensive than for N depositions and generally from the UK, where there is a clear negative relation between S deposition and species richness (Mitchell *et al.*, 2018; Tipping *et al.*, 2021; Seaton *et al.*, 2023). The link between S deposition and a corresponding shift towards a more acid-tolerant/acidophilic community composition is less well researched, with Seaton *et al.* (2023) finding that decreases in S deposition between 1978–2019 were reflected in corresponding changes in community composition and increases in soil pH in seminatural habitats, but not in intensive grasslands, which remained relatively stable throughout this period.

The exceedances of the critical loads of acidity due to S and N are limited compared to those of eutrophication, having hotspots in the Netherlands and some areas in Germany, Belgium, and Czechia, representing only 3% of ecosystem area across Europe in 2022 (EMEP, 2024). Similar to N depositions, S depositions in Europe increased with industrialisation but began to decrease already in the 1980s and 1990s due to initiatives to reduce pollution (Berge *et al.*, 1999; Aas *et al.*, 2019; Grennfelt *et al.*, 2020). Acid deposition occurs through both N and S, though S is the largest contributor on a global scale (Gao *et al.*, 2018), with S and N depositions tending to be highly correlated both globally as well as on a regional scale as deposition is strongly influenced by climatic patterns and conditions (Costa *et al.*, 2022; Benish *et al.*, 2022; Rubin *et al.*, 2023). The cycles of S and N are also known to be tightly linked, namely with gaseous ammonia reacting with atmospheric sulphuric acid to produce particulate ammonium and with nitrogen dioxide acting as a key oxidant of sulphur dioxide in aerosol water, producing sulphates (Dentener *et al.*, 2006; Cheng *et al.,* 2016). Therefore, when considering N depositions its effect on S depositions should also be taken into consideration.

1.3 Temperature changes

Temperature increase is the most apparent climatic change with a 3.1°C mean increase in Austria since 1880 (Formayer *et al.*, 2025). Furthermore, modelling from a recent study using HISTALP data (Auer *et al.*, 2007) has identified the late 1970s and early 1980s as the timespan corresponding to the beginning of the rapid increase in temperatures in Austrian lowlands, with a 0.5°/decade increase (Formayer *et al.*, 2025). Annual temperatures have indeed been rising in Europe for several decades, with Twardosz *et al.* (2021) pinpointing 1985 as the year following which air temperature increased linearly, with Van der Schrier *et al.* (2013) estimating Europe's rate of warming between 1980–2010 to be 0.41°C per decade. Seasonal precipitation dynamics have changed too, mainly towards drier summers and wetter winters (Rowell, 2005; Christidis & Scott, 2022). Together, temperature and precipitation changes have led to strong and longer drought events (Spinoni *et al.*, 2018; Grillakis, 2019).

Generally, increasing temperatures and associated drying have been shown to promote the growth and range expansion of some generalist species and particularly of thermophilic and xerophilic species compared to species less well-adapted to warm and dry conditions (Vesperinas *et al.*, 2001; Moradi *et al.*, 2012; Oldfather & Ackerly, 2019). The shift towards more thermophilic communities in Swiss grasslands over time found by Häberlin & Dengler (2025) was linked to increasing temperatures as well as longer summer drought periods, though there was no overall change observed in the communities' soil moisture indicators, suggesting that other factors play a role. Soil moisture was, however, found to decrease over time on high-elevation plots, supported by evidence that temperature increases due to climate warming are greater in mountainous regions (Nogués-Bravo *et al.*, 2007; Engler *et al.*, 2011). Thermal conditions have further been shown to be highly predictive of biodiversity distribution patterns in the Austrian Alps (Moser *et al.*, 2005). In a study by Klinkovská *et al.* (2025) using resurvey data of various Czech grassland habitats, it was found that in dry habitats mesophilic species increased over time in spite of higher temperatures and more frequent drought events. The authors also note that changes in community composition may be delayed with regard to the causal climate warming (Bertrand *et al.*, 2011) or communities' microclimatic conditions may buffer macroclimatic effects (De Frenne *et al.*, 2013a; Lenoir *et al.*, 2013). Taken together, the effects of rising temperatures on species numbers alone in a given region is therefore likely to depend on various factors, such as the habitat type, biogeography, and existing community composition.

The effects of N deposition on ecosystems strongly interact with climatic changes (Porter *et al.*, 2013; Dirnböck *et al.*, 2017; Hämmerle *et al.*, 2018). For example, Boutin *et al.* (2017) linked the observed increase in species richness in Pyrenean subalpine grasslands to the increases in both N deposition and temperature, while Roth *et al.* (2019) found that the gain of eutrophic and loss of oligotrophic species due to N deposition had a lesser effect on community composition than did climate warming. So, while the concrete mechanisms between the two

are not fully understood, it seems reasonable that long-term effects on plant communities cannot be studied without considering both climate and deposition.

1.4 Research objectives and aims

The aim of this study was to use existing spatio-temporal datasets of N deposition, S deposition, and temperature in Austria, alongside vegetation data spanning the last ca. 100 years to explore the effects of N and S depositions, as well as changes in temperature on grassland communities. As Austria's grasslands contain many rare and endangered plant species, they present a key ecosystem group on which the effects of airborne N and S, alongside increasing temperatures merit investigation (Ellenberg, 1998). There is little to no published research in this area, namely investigating the long-term effects of N and S depositions on Austrian grasslands, but comparable research in the same field addressing other vegetation classes, such as forest habitats (e.g., Hülber *et al.*, 2008; Jandl *et al.*, 2012), or focusing on grasslands but in other countries/regions (e.g. Duprè *et al.*, 2010; Stevens *et al.*, 2010a; Roth *et al.*, 2013, 2015; Storkey *et al.*, 2015). Hypotheses were thus defined according to each predictor variable and also to address differences between grassland types.

Hypothesis 1: nitrogen depositions are i) positively correlated with species number at low levels of deposition and negatively correlated at moderate to high levels, and ii) associated with a shift towards more nitrophilic/eutrophic species and more acidophilic species.

Hypothesis 2: sulphur depositions are i) negatively correlated with species number, and ii) associated with a shift towards more acidophilic species.

Hypothesis 3: the magnitude of temperature increase i) has a variable effect on species richness which depends on the grassland type, and ii) is associated with a shift towards more thermophilic species and more xerophilic species.

Hypothesis 4: Alpine and subalpine grasslands are expected to be more sensitive to increases in temperature, while nutrient-poor grasslands (across all elevations) are expected to be more sensitive to N depositions, and grasslands on base-rich soils with high buffering capacity are expected to be less sensitive to acidification through N and S deposition.

2. Methods and materials

2.1 Vegetation classes

Our approach is based on complete lists of species growing together in communities of 0.1–1020 m² in size (mean: 34 m²), so called vegetation plots. These vegetation plots were classified into different grassland types, following the typology of 'vegetation classes' in the syntaxonomical system of Austrian plant communities (Mucina *et al.*, 1993; Grabherr & Mucina, 1993). I selected these classes on the basis of their prominence in Austria and the availability of data, with a focus on nutrient-poor grassland types where the effects of nutrient addition are expected to be more pronounced (e.g., Bobbink *et al.*, 1998; Bobbink *et al.*, 2022). Brief descriptions of the key features of the selected vegetation classes follows, as described in the EuroVegChecklist and other literature (Ellenberg, 1988; Niklfeld, 1993; Mucina *et al.*, 2016).

Festuco-Puccinellietea Soó ex Vicherek 1973, abbreviated FEP henceforth, are inland saline steppes and grasslands with a broad distribution across continental Europe. FEP communities typically feature halophytic perennial species, comprising both hypersaline dry soils as well as mesic, wet soil types such as solonchak. In Austria, FEP communities are distributed in northern Upper and Lower Austria, as well as in eastern Lower Austria and northern Burgenland. (e.g. eastern Pannonian areas, southern Alps).

Festuco-Brometea Br.-Bl. et Tx. ex Soó 1947, FES, are dry grasslands and steppes with a distribution ranging from the hemiboreal regions of Europe, across temperate Europe, to sub-Mediterranean regions. The class is largely composed of communities growing on nutrient-poor and base-rich calcareous soils, though some communities grow on base-poor soils. It is characterised by species-rich communities with many thermophilic species adapted to the dry conditions. The FES class is distributed throughout all of Austria.

Loiseleurio-Vaccinietea Eggler ex Schubert 1960, LOI, are alpine heathlands and arctic scrublands distributed in the arctic tundras and alpine zones of Eurasia. The alpine heathlands are populated by dwarf-heaths and other acidophilic species and generally grow on base-poor soils. In Austria, LOI is broadly distributed through the eastern and southern regions reaching to the southern borders of Upper and Lower Austria.

Juncetea trifidi Hadač in Klika et Hadač 1944, JUN, are alpine grasslands distributed throughout alpine regions in the nemoral zones of Europe, Siberia, the Caucasus, and the arctic zones in northern Europe. The class is characterised by base-poor soils like on siliceous bedrock and is associated with acidophilic species. The JUN class has much the same distribution in Austria as the LOI class, often being found in mosaic habitats with one another, both being alpine communities growing on base-poor soils. Based on this overlap the two vegetation classes were combined under the 'LOI' label.

Molinio-Arrhenatheretea Tx. 1937, MOL, are meadows, mesic pastures, and meadow-fringes characterised by secondary vegetation as a result of anthropogenic management. They have a pan-European distribution, occurring predominantly at low and intermediate elevations on fertile soils, making MOL the sole vegetation class typically associated with nutrient-rich conditions in this study. The MOL class is distributed throughout Austria, with hotspots in western Vorarlberg, in Lower Austria around the periphery of Vienna, in Burgenland, and along the border between Upper Austria and Salzburg.

Nardetea strictae Rivas Goday et Borja Carbonell in Rivas Goday et Mayor López 1966, NAR, are secondary mat-grass (*Nardus stricta* L.) grasslands distributed from temperate to boreal regions of Europe at low and intermediate elevations. The NAR class is characterised by nutrient-poor and base-poor soils and is distributed throughout all of Austria.

Calluno-Ulicetea Br.-Bl. Et Tx. ex Klika et Hadač 1944, ULI, are *Nardus* and *Ulex* grasslands and heathlands distributed throughout the temperate to boreal regions of Europe at low to montane elevations. Similarly to the NAR class, ULI is also characterised by nutrient-poor and base-poor soils with a distribution throughout Austria, though being relatively rare; for this reason, these two vegetation classes were combined under the 'NAR' label.

Elyno-Seslerietea Br.-Bl. 1948, SES, are montane to alpine grasslands distributed throughout the nemoral zones of temperate mountain ranges in Europe. The class is characterised by species-rich communities growing on base-rich calcareous soils. Similar to LOI and JUN, SES is distributed throughout the eastern and southern regions of Austria, reaching northward just across the borders of Upper and Lower Austria.

Carici rupestris-Kobresietea bellardii Ohba 1974, KOB, are arctic-alpine Bellardi bog sedge (*Carex myosuroides* Vill.) grasslands and dwarf-scrub alpine slopes and tundra distributed in the alpine and arctic belts of mountain ranges in boreal and nemoral regions of Europe. The class is characterised by base-rich soils and has a very similar distribution in Austria to SES, though occurring far less frequently. Thus, in combination with the shared features of base-rich soils and alpine communities, the classes KOB and SES were combined under the 'SES' label.

2.2 Data handling and per-plot calculations

2.2.1 Vegetation data

The vegetation survey plot dataset used was composed of over 280 individual datasets, ranging from 1927 to 2024, from both published and unpublished sources from the Austria Vegetation Database (www.givd.info/ID/EU-AT-001; Willner *et al.*, 2012). For each plot, all plant observations, i.e. a complete list of vascular plant species, and various supplementary

information such as geographic position, year of recording, vegetation class, and surface area were given.

Following assembly into one large dataset with 468,496 individual taxon observations across 14,546 plots the data was cleaned, removing four plots with insufficient information and removing any non-tracheophyte taxon observations, such as lichens, bryophytes, and fungi. The resulting dataset comprised 445,892 individual taxon observations. Taxonomic harmonisation was then carried out using Karrer's list of ecological indicator values for Austrian tracheophytes (Karrer, 2024) as a reference, which itself uses the updated nomenclature from the as yet unpublished fourth edition of the "Exkursionsflora für Österreich, Liechtenstein, Südtirol" ("Excursion flora for Austria, Liechtenstein, South Tyrol"; *cf.* Fischer *et al.*, 2008). Ecological indicator values define the conditions for optimal growth of a given species, thereby allowing inferences to be made about the environmental conditions in a given area when on site physico-chemical measures are not available. Approximately 92.5% of all tracheophyte taxon observations were successfully matched to a taxon in Karrer's indicator value list, with nomenclature being updated where appropriate and any remaining unmatched observations left unchanged.

For each plot the alpha biodiversity was calculated using all individually recorded taxa. For each plot the mean ecological indicator values for nutrients (N), temperature (T), reaction (R), and moisture (F) were calculated using taxon observations matched to the indicator reference list (Karrer, 2024). We did not weigh species by their abundance. Any taxon observations with non-numeric indicator values, such as the values of "indifferent" or "bimodal", were excluded from these calculations. For each plot a further metric, labelled 'Ratio N', was calculated as the common logarithm of the ratio of the number of oligotrophic taxa to eutrophic taxa. Oligotrophic taxa are defined as having N-values between 1–4 and eutrophic taxa as having N-values between 6–9. To avoid undefined Ratio N values, instances of 0 recorded oligotrophic or eutrophic taxa were set to 0.5.

2.2.2 Deposition data

Total annual deposition data for both N and S spanning 1990–2023 with a spatial resolution of 0.1° was acquired directly from EMEP (2020). Values for the year 2024 were calculated as the mean of 2022 and 2023. Data for seminatural vegetation were used, this representing the most appropriate receptor ecosystem type. Historical annual N and S deposition data spanning 1880–2020 complemented the EMEP data (Schöpp *et al.*, 2003). The historical data was only used for the timeframe of 1880–1989. The data were then converted to either kg N ha^{-1} a^{-1} or kg S ha^{-1} a^{-1} respectively, and wet and dry depositions were summed together for both N and S respectively. In the case of N, reduced and oxidised N depositions were summed together.

For each plot a baseline deposition value for both N and S respectively was calculated given by the accumulated annual deposition between 1880–1909, representing an early-industrial 30-year accumulation baseline as described in Rashid *et al.* (2023). Note that it is assumed that the pressure of S deposition on vegetation can be treated like the one of N depositions. For each plot the summed deposition in the past 30 years relative to the plot's year of recording was calculated, representing the 30-year accumulation window. The anomaly between the baseline deposition and the 30-year accumulation window was calculated for both N and S for each plot, termed ΔN and ΔS respectively.

2.2.3 Temperature data

Mean annual temperature data spanning 1961–2024 with a spatial resolution of 1 km was acquired directly from the SPARTACUS (v.21) dataset (Hiebl & Frei, 2016). Historical mean annual temperature data spanning 1901–2024 with a spatial resolution of 0.5° was acquired from the CRU (TS v. 4.09) dataset (Harris *et al.*, 2020). A mismatch between the two datasets when comparing data available for the same timeframe, 1961–2024, was evident, so we harmonised the two by way of a linear regression. We regressed the 1961–1980 SPARTACUS data against CRU data of the same timeframe, allowing SPARTACUS values to be predicted for the timeframe of 1901–1960 on the basis of the CRU values.

Following this, for each plot a baseline temperature was calculated given by the mean annual temperature between 1961–1980. We chose this time frame because it spans the last two decades before the onset of recent pronounced warming in Austria (Formayer *et al.*, 2025). For each plot the mean annual temperature in the past 20 years relative to the plot's year of recording was calculated, representing a 20-year temperature window. The anomaly between the baseline temperature and the 20-year temperature window was calculated for each plot, termed ΔT.

2.3 Random forest modelling

The resulting data matrix was then used for random forest modelling in R Studio Team (2020) using the ranger package (Wright & Ziegler, 2017). The models took the following general form:

$$\text{Response variable} \sim \text{Predictor variables}$$

where the response variable may be alpha biodiversity, mean N, mean T, mean R, mean F, or Ratio N. The predictor variables are baseline N deposition, baseline S deposition, baseline

temperature, ΔN, ΔS, ΔT and vegetation class. When modelling the response of alpha biodiversity, plot surface area was added as a covariate.

The data was first randomly stratified into six strata such that the global distribution of the six vegetation classes was maintained within each stratum. Subsequently, further random stratification into high-ΔN and low-ΔN using the median ΔN within each vegetation class was performed, followed by the analogous random stratification by ΔT. The data, now as 24 strata, was then randomly split into 90% model training data and 10% used to evaluate the model. This process and all subsequent modelling processes were repeated across 10 seeds, with all results given by the means of these seeds.

Hyperparameter tuning was conducted for the hyperparameters 'mtry' (the possible number of variables to split at in each node) and 'min.node.size' (the minimum node size for splitting). Fixed hyperparameters of 1000 trees ('num.trees') and the importance 'permutation' were used. The values tested for mtry were 2, 3, 4, 5, 6, and 7 and those for min.node.size were 2, 5, 10, and 15. Error statistics and importance scores for each of a model's predictors were generated using all possible combinations of these hyperparameters for each response variable. The optimal hyperparameter combinations for each response variable were selected on the basis of the lowest root mean square error and employed for all future models (Table S1, Table S2).

After fitting the models, predictions were made in turn for each unit of ΔN, ΔS, and ΔT, both overall and per vegetation class. We did not make predictions for all response variables with each Δ, but only for those responses where we expected a direct effect (such as, e.g. ΔN on species richness or mean N). In all models, the three baseline predictors and plot surface area, where applicable, were set to the median value within each given vegetation class. For each prediction for a given Δ, said Δ was set to a sequence of 100 values evenly spaced across its full globally observed range, whilst the other two Δ predictors were set to 0. Predictions were also made for combinations of two Δs for each vegetation class, where a 'primary' Δ was set to a sequence of evenly-spaced 100 values as above, while a 'secondary' Δ was set a sequence of four levels given by the 25th, 50th, 75th, and 100th percentile values of the 'secondary' Δ within each given vegetation class, termed 'lowest', 'lower', 'higher', and 'highest' respectively.

Relative effect sizes were calculated for individual predictions using the following formula:

$$Relative\ effect\ size = \frac{pred\Delta_{max} - pred\Delta_{min}}{pred\Delta_{min}} \times 100\%$$

where $pred\Delta_{min}$ and $pred\Delta_{max}$ give the predicted value of the response variable at the lowest and highest values of the Δ in question respectively. These values reflect the real observed ranges

of each Δ for a given vegetation class, i.e., using vegetation class-specific extrema Δ values, not the global extrema.

The prediction results were then plotted as curves and heatmaps of the relative effect sizes were generated.

3. Results

3.1 Spatio-temporal distribution of the plots in Austria

The spatial distribution of the plots (Fig. 1) was found to be broadly even, with no obvious gaps in the data, though some regions showed a lower density of plots, such as the upper Innviertel of Upper Austria, the area around Ziller Valley, and in the periphery of Graz. Other areas such as Vienna's periphery, and western Vorarlberg, showed a very high density of plots.

The temporal distribution of the plots (Fig. 1A) was found to be less evenly distributed, with the majority of plots having been surveyed between 1970–2019. This can largely be accounted for by the fact that studies using such vegetation survey data became increasingly popular throughout the 20th century, as well as much older data not being readily available, especially in a format conducive to this study. Some spatial patterns were observed, such as the majority of the plots in southern Carinthia having been surveyed before 1940, clusters of plots in Tyrol having all been surveyed in the 1960s, and plots from Vienna's periphery generally having been surveyed since 1990. Patterns in the spatial distribution of plots according to their vegetation classes were reflective of their natural observed distributions in Austria (Fig. 1B).

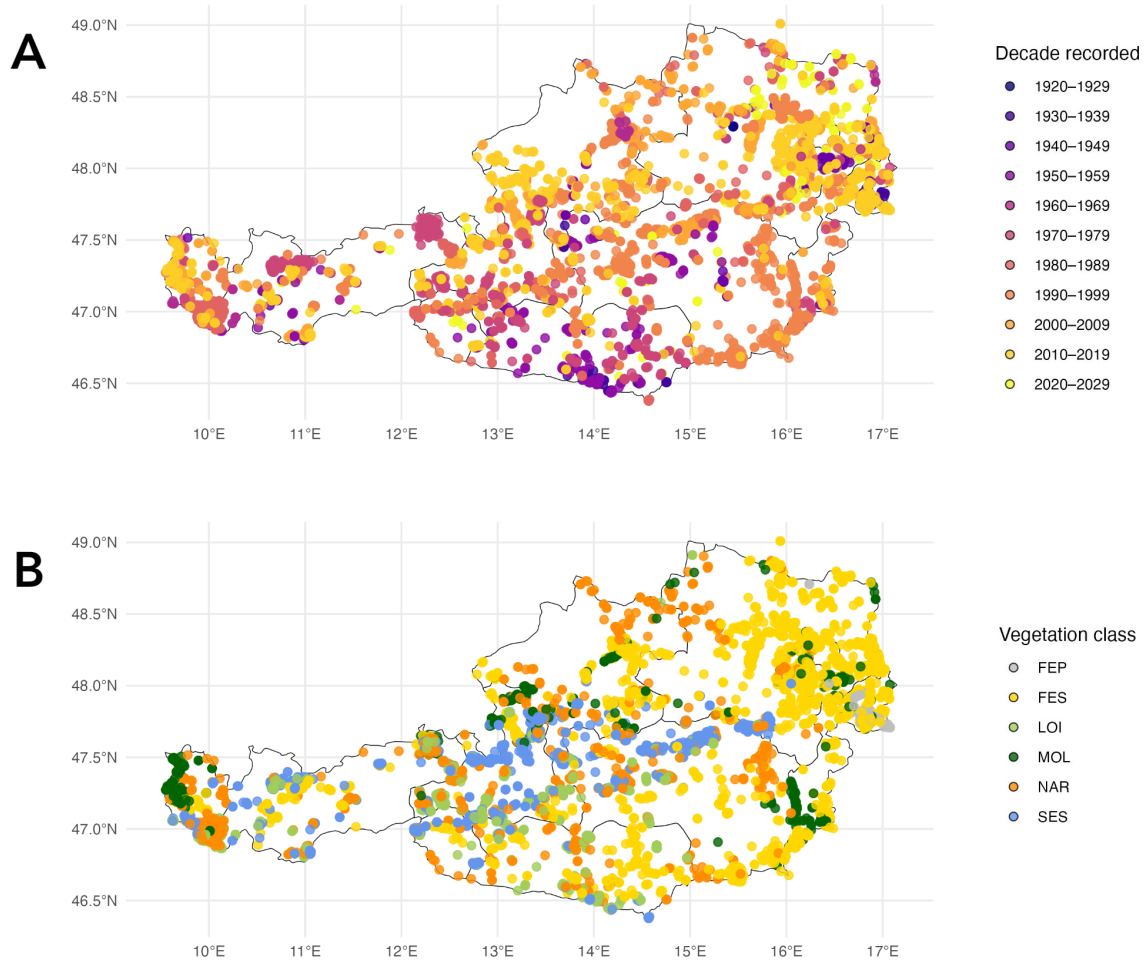

Figure 1: Maps of Austria with the location of each vegetation plot surveyed denoted by a circle coloured according to (A) the decade when the plot was surveyed and (B) the plot's vegetation class. Vegetation classes: FEP - *Festuco-Puccinellietea*, FES - *Festuco-Brometea*, LOI - *Loiseleurio-Vaccinietea* and *Juncetea trifidi,* MOL - *Molinio-Arrhenathere*tea, NAR - *Nardetea strictae* and *Calluno-Ulicetea*, SES - *Elyno-Seslerietea* and *Carici rupestris-Kobresietea bellardii.*

3.2 Distributions of the Δs

The ΔN values were found to be distributed unimodally (Fig. 2) with a peak around ~220 kg N ha^{-1} and with 92.9% of all values falling between 0–400 kg N ha^{-1}, while only 1.6% of values were below 0 kg N ha^{-1} (i.e. denoting a decrease in deposition relative to the baseline). The distribution curve of the ΔS values resembled that of the ΔN values, though with two peaks instead of one, at ~200 and ~850 kg S ha^{-1}. The majority of ΔS values lay between these two peaks, with 97.4% of all values falling between 0–1500 kg S ha^{-1}, with only 1.8% values below 0 kg S ha^{-1}. The distribution of ΔT values was found to be strongly skewed to the left, peaking at ~0.05°C and tapering off approaching 2.0°C, with 8.9% of values below 0.0°C.

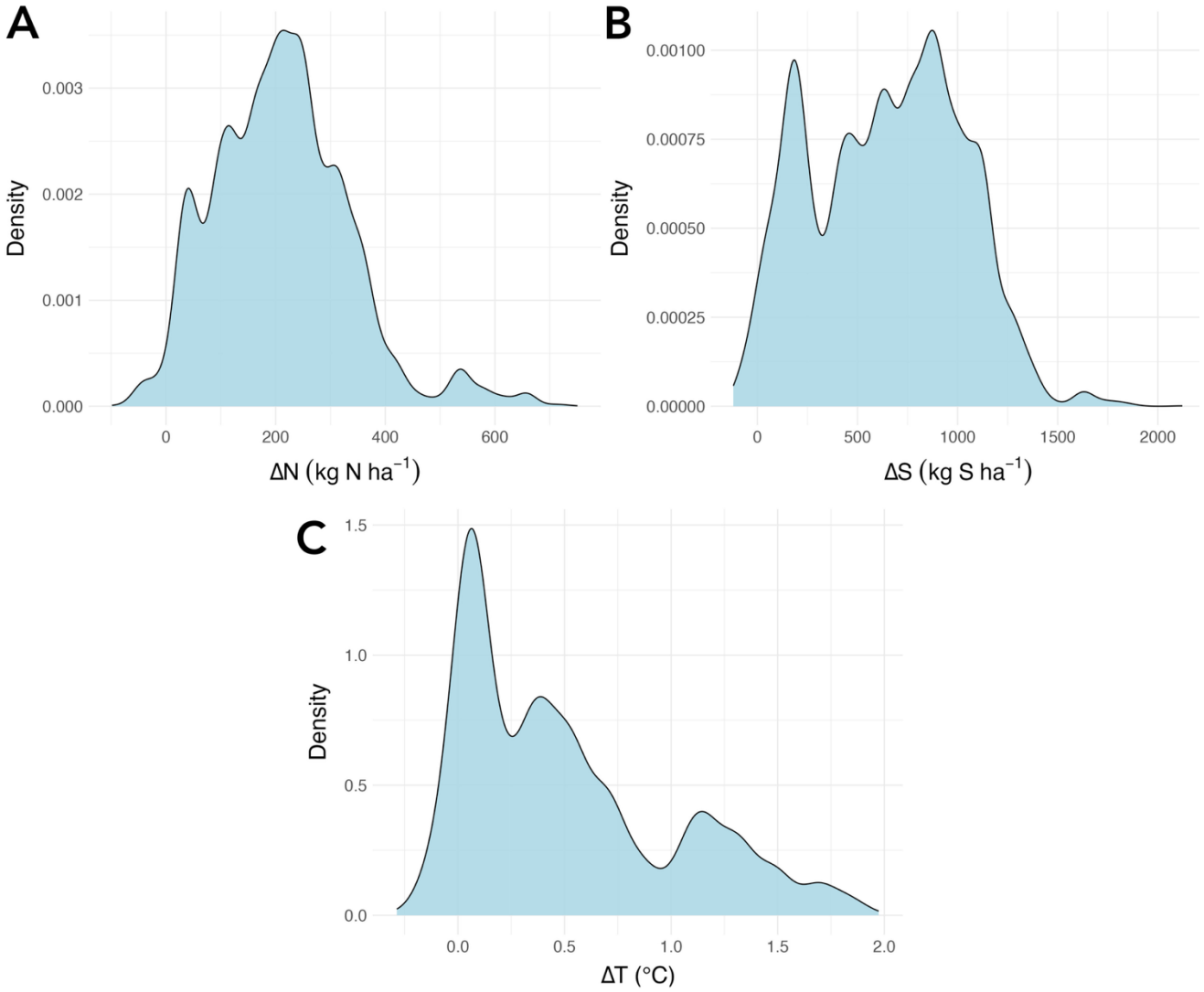

Figure 2: Density plots of the distributions of (A) ΔN (kg N ha^{-1}), (B) ΔS (kg S ha^{-1}), and (C) ΔT (°C) across all surveyed plots.

3.3 Summary statistics of all models

The summary statistics showed that most models had a strong fit, being able to explain a high percentage of variation in the data, with the R-squared values ranging from 0.58–0.97 (Fig. 3).

The RMSE of the alpha biodiversity model of 8.2 was moderately high compared to its standard deviation of 14. The related Mean N and Ratio N models also had relatively high RMSEs of 0.45 and 0.33 given their standard deviations of 0.84 and 0.52 respectively. The remaining models (Fig. 3D–F) had RMSEs between 0.28–0.50, which may be considered intermediate given their standard deviations ranging from 1.1–1.7.

Baseline temperature and vegetation class were found to be the two consistently most important predictors in all indicator value-based models (Fig. 3B–F), with baseline S consistently ranking third in importance. Moreover, baseline temperature was found to be the most important predictor in the alpha biodiversity model, followed by plot surface area and baseline N. The alpha biodiversity model showed the most even spread of importance scores across predictors, whereas all predictors of mean T-values, barring baseline temperature and vegetation class, were of negligible importance. The Δ predictors predominantly ranked lowest in importance out of all predictors, with ΔN generally ranking higher than the other Δs, particularly in the mean N and Ratio N models.

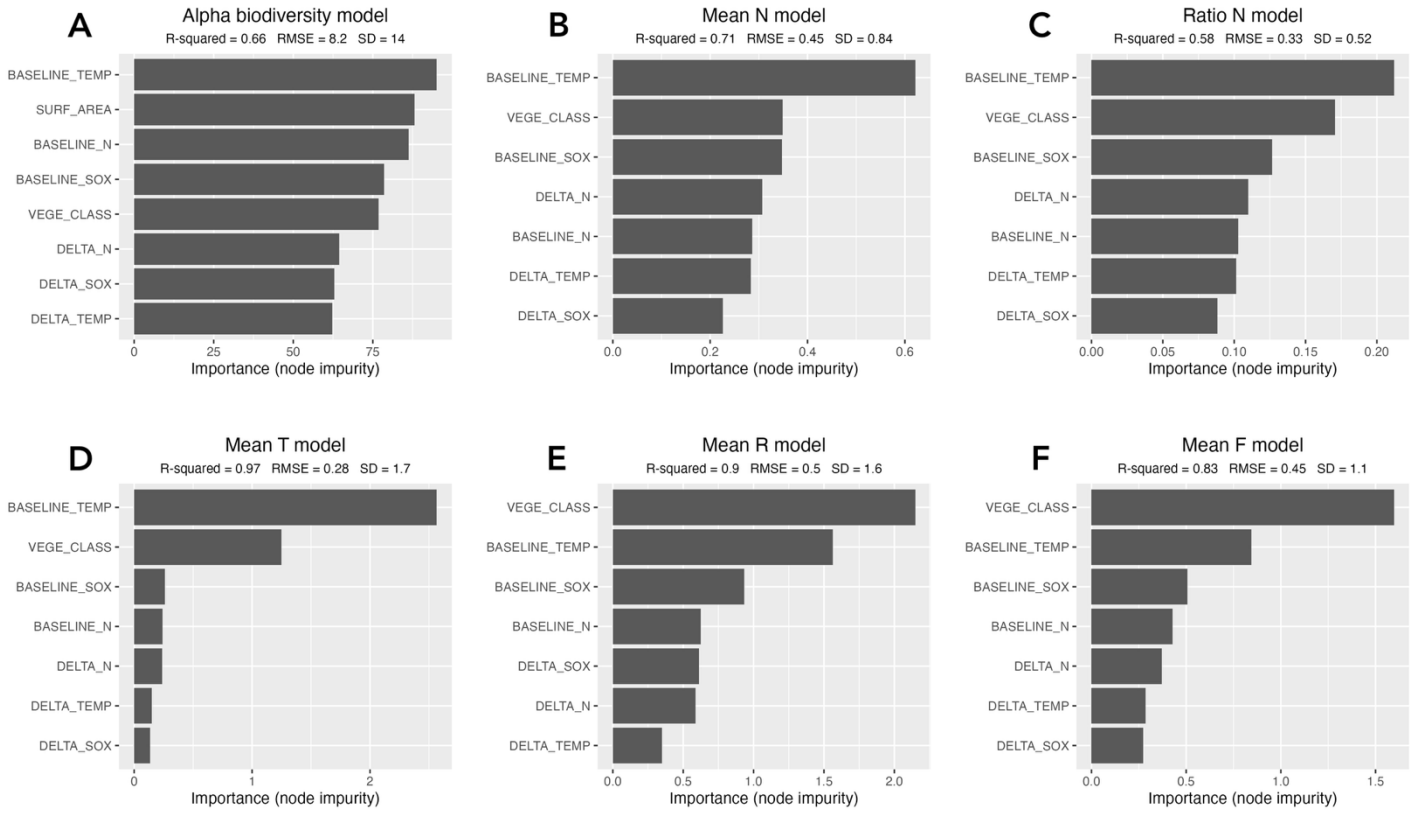

Figure 3: Predictor importance barplots in descending order of predictor variable importance for the response variable of (A) alpha biodiversity, (B) mean N, (C) Ratio N, (D) mean T, (E) mean R, and (F) mean F. The R-squared value, root mean square error (RMSE), and standard deviation of actuals (SD) are given for each respective model. Ratio N = $\log_{10}$ of the ratio of the number of species with N-values 1–4 to those with N-value 6–9.

3.4 Correlation analyses of Δs and mean indicator values

All three combinations of Δs, with data taken from all plots, showed varying degrees of correlation, with correlations within vegetation classes generally clustering closely around the overall correlation (Table 1, Table S3).

A moderately strong positive correlation between ΔN and ΔS across all vegetation classes was found, $r(14540) = 0.509$, $p < 0.001$, while a weaker total correlation between ΔN and ΔT was found, $r(14540) = 0.302$, $p < 0.001$. The total correlation between ΔS and ΔT was found to be moderately negative, $r(14540) = -0.394$, $p < 0.001$.

Table 1: Pearson's correlation coefficients (r) between pairs of predictor Δs across all vegetation survey plots, separately by vegetation class and overall. The magnitude of the correlation is also indicated by a colour from blue to red. The p-values and degrees of freedom for each predictor pair are given in Table S3.

	r						
Predictors	***FES***	***FEP***	***MOL***	***NAR***	***LOI***	***SES***	***Total***
ΔN - ΔS	0,550	0,628	0,198	0,510	0,792	0,613	0,509
ΔN - ΔT	0,176	0,462	0,577	0,202	0,283	0,235	0,302
ΔT - ΔS	-0,572	-0,373	-0,427	-0,468	-0,036	-0,251	-0,394

The indicator values, taken across all plots, showed variable correlations with one another (Table 2). Notably, a moderate correlation between mean N-values and mean T-values was found, $r(14539) = 0.461$, $p < 0.001$, mirroring the correlation between ΔN and ΔT. Moderate to weak positive correlations were also found between mean R-values with both mean T-values and mean N-values, $r(14539) = 0.490$, $p < 0.001$, and $r(14540) = 0.247$, $p < 0.001$ respectively. Mean T-values and mean F-values were found to be moderately negatively correlated, $r(14533) = -0.313$, $p < 0.001$.

Table 2: Pearson's correlation coefficients (*r*) between pairs of ecological indicator values across all vegetation survey plots. The magnitude of the correlation is also indicated by a colour from blue to red. The *p*-values and degrees of freedom for each predictor pair are given in Table S4.

Variable pair	***r***
Mean T - Mean F	-0,313
Mean T - Mean R	0,490
Mean T - Mean N	0,461
Mean F - Mean R	-0,355
Mean F - Mean N	0,420
Mean R - Mean N	0,247

3.5 Predictions for ΔN

Predictions for ΔN were made for the response variables of alpha biodiversity, mean R-value, mean N-value, and Ratio N (Fig. 4).

As shown in Fig. 4A, a positive total relative effect size (RES) of ΔN on species number of +7% was predicted, representing an increase in species number of ~2.3 across the global ΔN range. MOL was the only vegetation class to have a predicted negative value (-2%), whilst FEP had a very high positive value (+45%), corresponding to a predicted gain of ~3.3 species across its ΔN range. Note that FEP plots were only sampled on a very narrow ΔN range of 275 kg N ha^{-1} compared to the global range of 849 kg N ha^{-1}.

A positive total RES of ΔN on mean R-value of +8% was predicted (Fig. 4B). FES was the only vegetation class with a negative value (-5%). Conversely, LOI, NAR, and SES all had relatively high positive values (+31%, +15%, +23% respectively), all with similar curve profiles trending upwards until ~200 kg N ha^{-1} after which they plateaued.

The predictions for the related variables of mean N-value and Ratio N are shown in Fig 4C-D. A positive total RES of ΔN on mean N-values of +11% was mirrored by a negative total RES for Ratio N of -14%. Differences between vegetation classes were minimal for both response variables with the exception of FES, which had a strong positive RES on mean N-values (+11) and correspondingly strong negative RES on Ratio N (-35%).

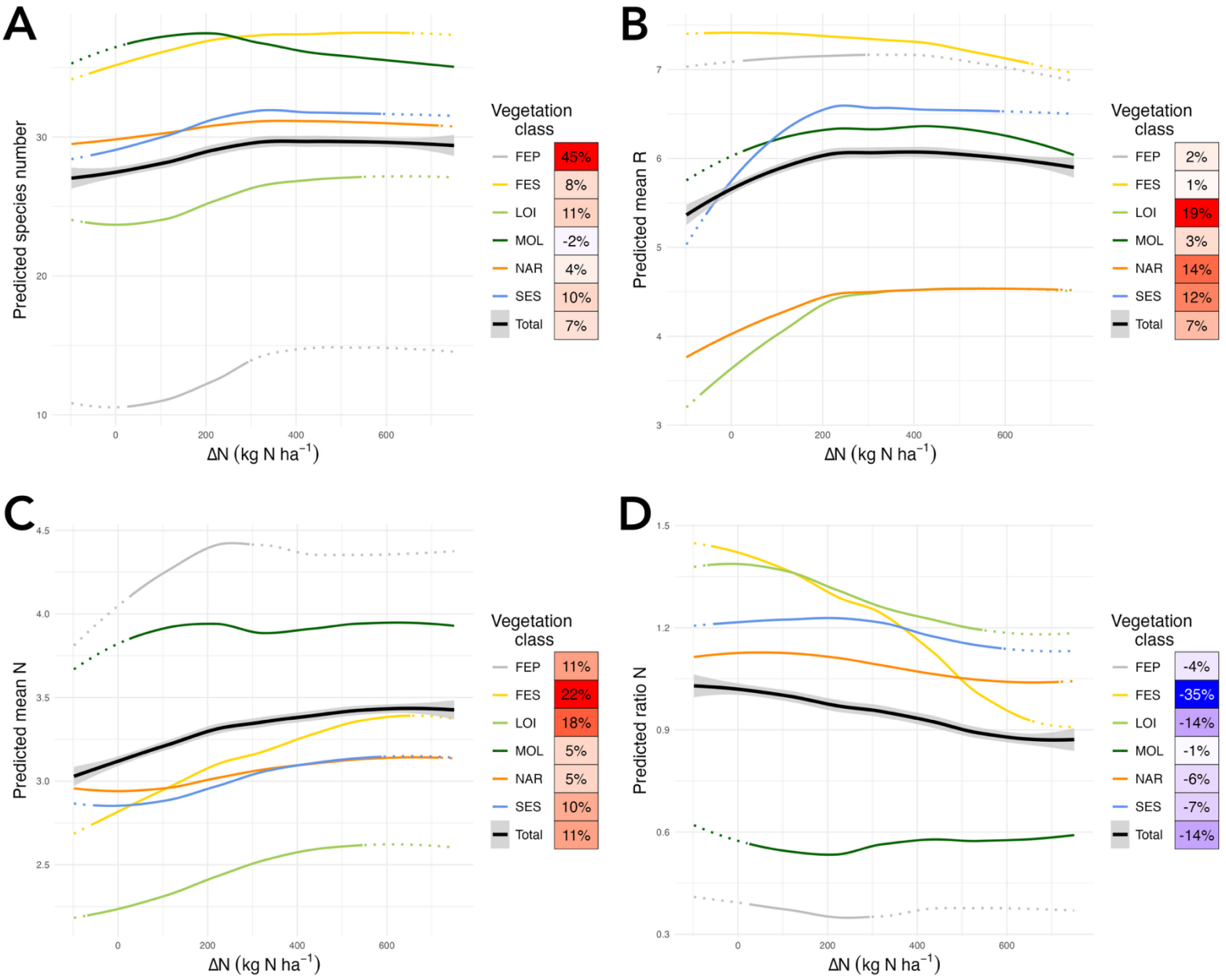

Figure 4: Model-based predictions for changes in (A) alpha biodiversity, (B) mean R, (C) mean N, and (D) Ratio N with ΔN (kg N ha^{-1}), the anomaly of the cumulative N depositions in the previous 30 years relative to the baseline accumulation between 1880–1910, for each of the six different vegetation classes and in total. The relative effect sizes for each curve are given as percentages and coloured according to magnitude. Solid lines denote the real observed range of ΔN for the given vegetation class; dotted lines denote ΔN values within the global range but not observed within the given vegetation class. A 95% confidence interval is given for the Total curve. Vegetation classes: FEP - *Festuco-Puccinellietea*, FES - *Festuco-Brometea*, LOI - *Loiseleurio-Vaccinietea* and *Juncetea trifidi,* MOL - *Molinio-Arrhenatheretea*, NAR - *Nardetea strictae* and *Calluno-Ulicetea*, SES - *Elyno-Seslerietea* and *Carici rupestris-Kobresietea bellardii.* 'Ratio N' = $\log_{10}$ of the ratio of the number of species with N-values 1–4 to those with N-value 6–9.

3.6 Predictions for ΔS

Predictions for ΔS were made for the response variables of alpha biodiversity and mean R-value (Fig. 5).

As shown in Fig. 5A, a weak positive total RES of ΔS on species number of +4% was predicted, representing a predicted gain of ~1.5 species across the global ΔS range. FES had a relatively high positive value (+16%) corresponding to a predicted gain of ~4.7 species across its ΔS range. All other vegetation classes had minimal predicted effect sizes.

Shown in Fig. 5B, a small positive total RES of ΔS on mean R-value of +7% was predicted. Similar to the predicted effects of ΔN of mean R-value, LOI, NAR, and SES had relatively high positive values (+19%, +14%, +12% respectively), all with similar curve profiles trending upwards until ~1250 kg S ha^{-1} after which they plateaued. The remaining three vegetation classes had minimal predicted effect sizes.

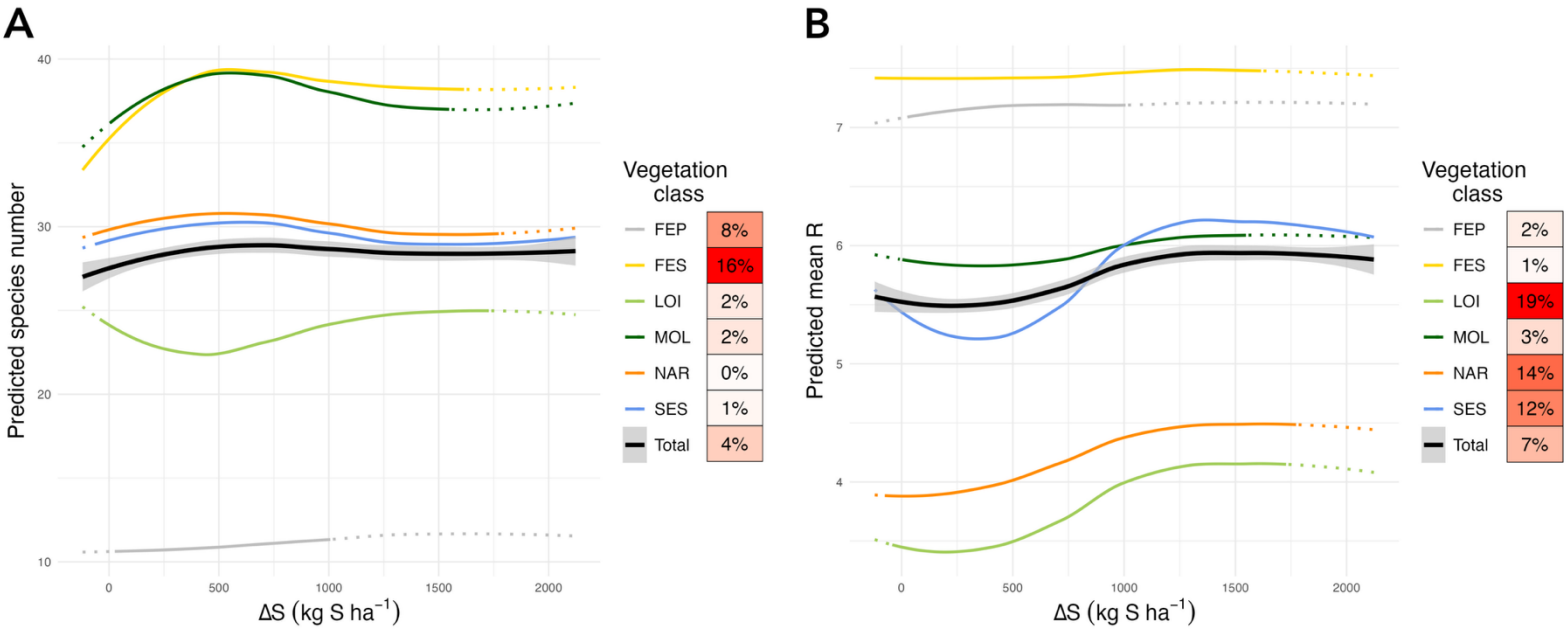

Figure 5: Model-based predictions for changes in (A) alpha biodiversity and (B) mean R with ΔS (kg S ha^{-1}), the anomaly of the cumulative S depositions in the previous 30 years relative to the baseline accumulation between 1880–1910, for each of the six different vegetation classes and in total. The relative effect sizes for each curve are given as percentages and coloured according to magnitude. Solid lines denote the real observed range of ΔS for the given vegetation class; dotted lines denote ΔS values within the global range but not observed within the given vegetation class. A 95% confidence interval is given for the Total curve. Vegetation classes: FEP - *Festuco-Puccinellietea*, FES - *Festuco-Brometea*, LOI - *Loiseleurio-Vaccinietea* and *Juncetea trifidi,* MOL - *Molinio-Arrhenatheretea*, NAR - *Nardetea strictae* and *Calluno-Ulicetea*, SES - *Elyno-Seslerietea* and *Carici rupestris-Kobresietea bellardii.*

3.7 Predictions for ΔT

Predictions for ΔT were made for the response variables of alpha biodiversity, mean T-value, and mean F-value (Fig. 6).

As shown in Fig. 6A, a negative total RES of ΔT on species number of -11% was predicted, though individual vegetation classes behaved very differently. FES and MOL both had relatively high negative values (-29% and a predicted loss of ~11.4 species; -22% and a predicted loss of ~8.6 species respectively across their ΔT ranges). Conversely, FEP and LOI both had relatively high positive values (+19% and a predicted gain of ~1.8 species; +23% and a predicted gain of ~4.5 species respectively across their ΔT ranges). The predicted effects for NAR and SES were minimal.

Shown in Fig. 6B, a small positive total RES of ΔT on mean T-value of +3% was predicted. LOI, NAR, and SES all had higher values (+15%, +15%, +7% respectively), with similar curve profiles, where an increase in predicted mean T-values occurred at ΔT values above 0.8°C. All other vegetation classes had minimal predicted effect sizes.

Shown in Fig. 6C, a negligible total RES of ΔT on mean F-values of +1% was predicted. FEP had a relatively high positive value (+11%), whereas FES had a relatively high negative value (-9%).

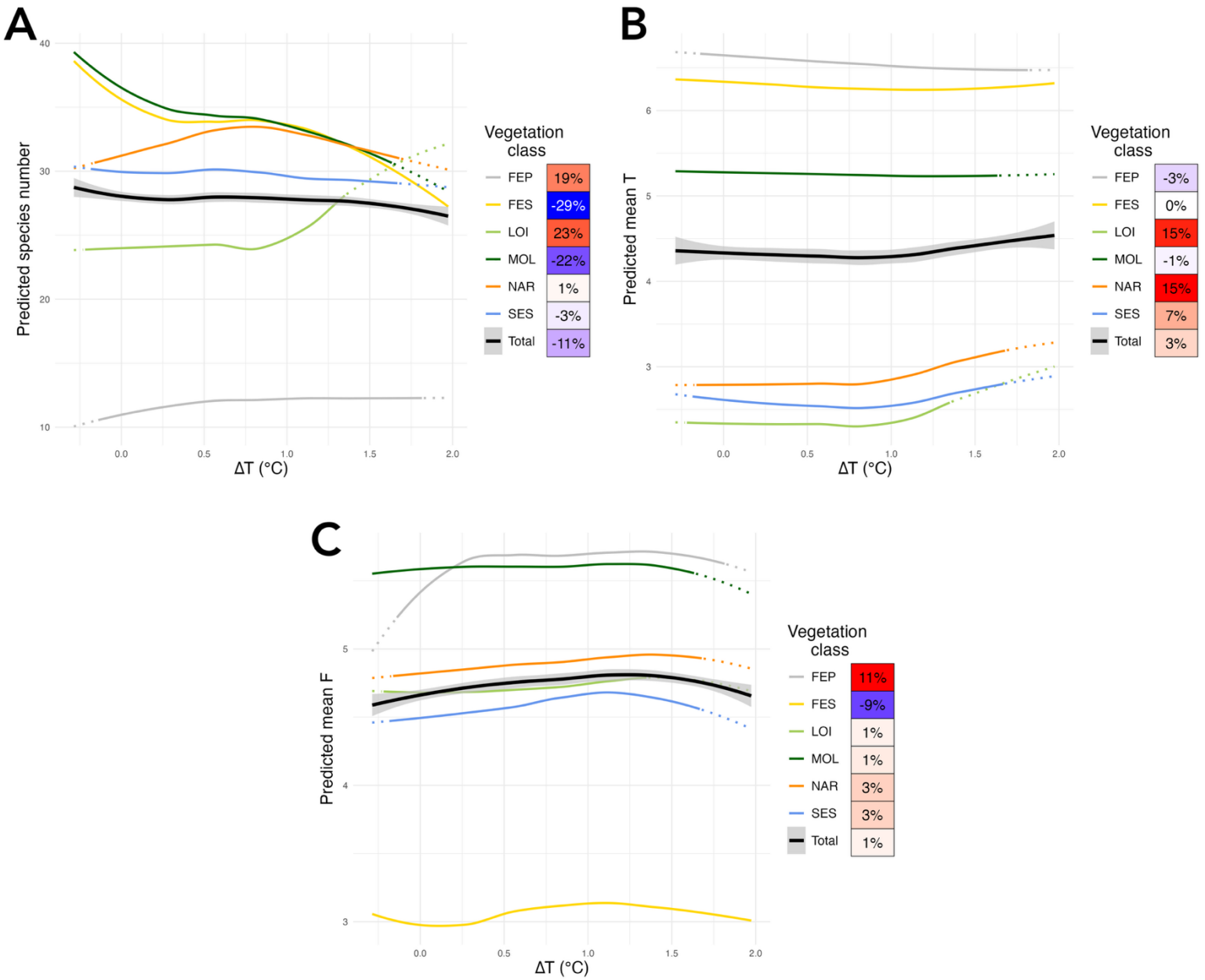

Figure 6: Model-based predictions for changes in (A) alpha biodiversity, (B) mean T, and (C) mean F with ΔT (°C), the anomaly of annual mean temperature relative to a baseline mean annual temperature between 1961–1980, for each of the six different vegetation classes and in total. The relative effect sizes for each curve are given as percentages and coloured according to magnitude. Solid lines denote the real observed range of ΔT for the given vegetation class; dotted lines denote ΔT values within the global range but not observed within the given vegetation class. A 95% confidence interval is given for the Total curve. Vegetation classes: FEP - *Festuco-Puccinellietea*, FES - *Festuco-Brometea*, LOI - *Loiseleurio-Vaccinietea* and *Juncetea trifidi,* MOL - *Molinio-Arrhenatheretea*, NAR - *Nardetea strictae* and *Calluno-Ulicetea*, SES - *Elyno-Seslerietea* and *Carici rupestris-Kobresietea bellardii.*

3.8 Interactions between different anomalies

No significant interactions between anomalies (Δs) were found for biologically meaningful and interpretable combinations of Δs and response variables. Lack of interaction was inferred by the four curves on a given graph having very similar profiles, differing only in their vertical position (Fig. 7A). In very few cases potential interactions were observed, as seen in Fig. 7B by the two different curve profiles with intersecting curves partitioned between the two lower and two higher ΔN levels. In these cases, however, the combinations of Δs, response variables, and given vegetation class were not deemed to be biologically meaningful or interpretable.

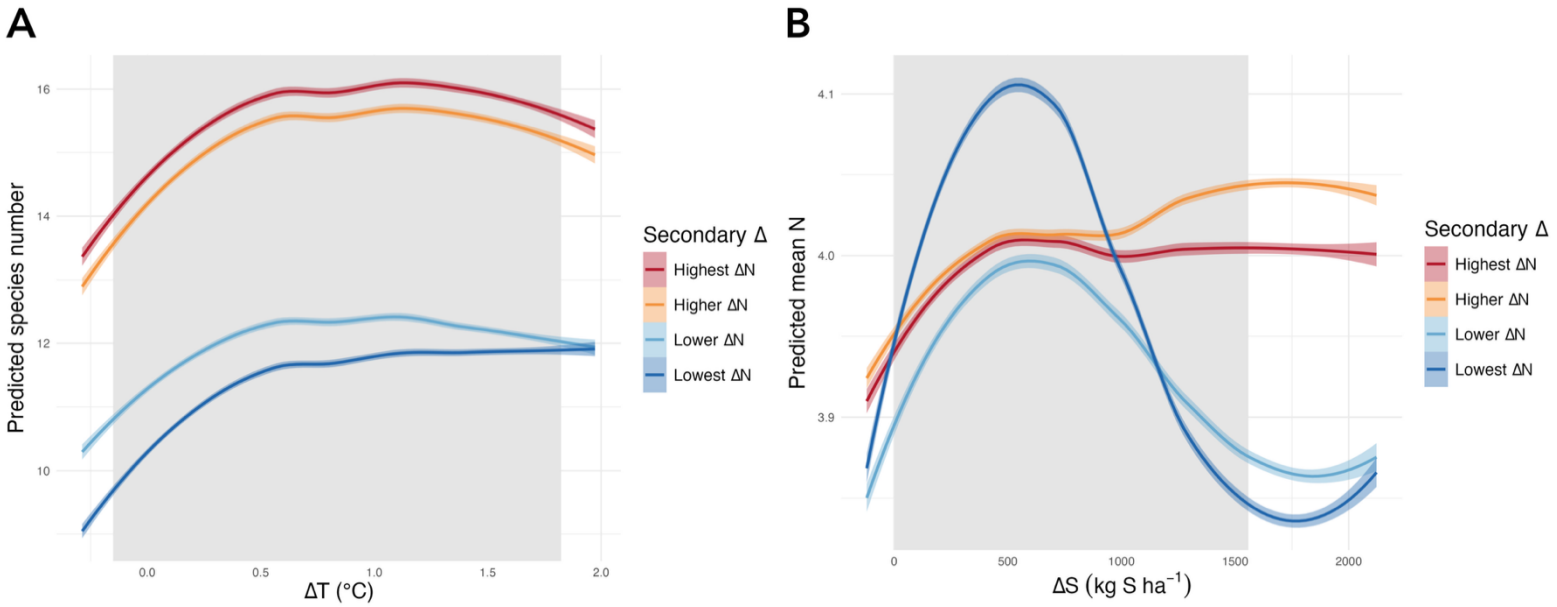

Figure 7: Model-based predictions for changes in (A) alpha biodiversity with ΔT (°C) at four different ΔN levels for the FEP vegetation class, and (B) mean N with ΔS (kg S ha^{-1}) at four different ΔN levels for the MOL vegetation class, where ΔN is the anomaly of the cumulative N depositions in the previous 30 years relative to the baseline accumulation between 1880–1910. The grey boxes denote the real observed range of ΔT and ΔS for the given vegetation classes respectively; dotted lines denote ΔT and ΔS values respectively within the global range but not observed within the given vegetation class. Confidence intervals of 95% are given for each curve. The four levels of the secondary Δ are given by the 25th, 50th, 75th, and 100th percentile values of this Δ within the given vegetation class, termed 'lowest', 'lower', 'higher' and 'highest' respectively. Vegetation classes: FEP - *Festuco-Puccinellietea*, MOL - *Molinio-Arrhenatheretea*.

4. Discussion

4.1 Trends and correlations in the models and data

The spatial and temporal distributions of the survey plots were broadly even, with some biases in the data being unavoidable given factors such as changing research priorities throughout time dictating which vegetation classes or regions are of interest. Clear spatial patterns in the distribution of the plots' vegetation classes are of course primarily dictated by their natural distribution, though other factors such as administrative borders likely play a role (notably MOL plots at the Styrian-Burgenland border). It is further worth noting that with the given data there may exist a tendency to underestimate the effect of climate change as a significant portion (~26%) of the data predates the 1980s.

While most of the models fit the data very well, some models showed higher predictive power than others, with the alpha biodiversity model likely having the lowest predictive power. By examining the importance scores of each of the models, it is apparent that baseline temperature is the single most important predictor when considered across all models. Other research supports temperature being a key ecological predictor for various vegetation metrics, though research with the same combination of predictors of temperature, and N and S depositions is sparse (Moles *et al.*, 2014; Butterfield & Munson, 2016; Guitar *et al.*, 2016).

The high importance of vegetation class as a predictor for all indicator value-based models is unsurprising and highlights the necessity to consider each vegetation class separately, as individual differences between them may result in misleading overall predictions. This was notably observed to be the case for the effect of ΔT on alpha biodiversity, where individual vegetation classes behaved very differently, resulting in an intermediate overall value. The high importance of surface area as a predictor for alpha biodiversity is evidently supported by the species-area relationship (Connor & McCoy, 1979). Research by Dubuis *et al.* (2012) in the Swiss Alps on predominantly calcareous soils found that N content and pH (here approximated with indicator R values) were the two most important predictors from a number of edaphic variables on plant community composition and species distribution, underlining the link between vegetation class and nutrient conditions.

It was also generally observed that baseline predictors had a greater importance compared to their corresponding Δ predictors, implying that baseline conditions determine both past and current values of response variables more than anomalies.

The interconnectedness of the predictors must nonetheless be carefully considered before further interpretating the results. A correlation analysis between the Δ predictors was carried out to address this, revealing ΔN and ΔS to be moderately correlated ($r = 0.509$), in line with the expectations that their depositions strongly depend on climatic patterns and conditions, namely wind and precipitation (Costa *et al.*, 2022; Benish *et al.*, 2022; Rubin *et al.*, 2023).

The weak positive correlation found between ΔN and ΔT (r = 0.302) may be due to altitude effects. Precipitation generally increases with altitude in mountainous areas (e.g. Ballantyne, 1983; Basist *et al.*, 1994; Johnson & Hanson, 1995; as summarised in Wang *et al.*, 2018) and in line with this N deposition would be expected to increase at higher altitudes. This, combined with the fact that higher elevations are expected to experience stronger temperature increases (e.g. Beniston & Rebetez, 1996; Beniston *et al.*, 1997; as reviewed in Gobiet *et al.*, 2014), could explain the positive correlation between ΔN and ΔT.

Lastly, the moderate negative correlation between ΔS and ΔT (r = -0.394) proves to be more puzzling, however, contradicting the above argument for N depositions. These apparently divergent interactions between the three Δs could be speculatively attributed to complex interactions between precipitation patterns and the sources of both N and S emissions, resulting in the observed correlations. This could, for example, help explain the differences in the relatively low levels of depositions in the periphery of Vienna compared to the relatively high levels in large areas of Upper Austria; though both regions are highly industrialised, i.e. sources of N and S emissions (STATISTIK AUSTRIA, 2022), Upper Austria receives far more precipitation than the periphery of Vienna (Hiebl & Frei, 2018).

4.2 Nitrogen depositions

4.2.1 Alpha biodiversity ~ ΔN

The predicted effect size of any given Δ on any given response variable across all predictor-response combinations was consistently and expectedly small relative to the absolute value of the response variable. It is worth noting that the overall values are given by the arithmetic mean across all plots, such that certain vegetation classes contribute to the total more than others (e.g. FES constitutes 37.8% of all plots). This, coupled with the fact that the plot data is not completely spatially homogeneous, means that the total values cannot be formally considered 'overall values for Austria' but rather are only indicative of general trends across vegetation classes.

The general increase in species number with increasing N deposition is only partially in line with expectations, with the results suggesting that N input alleviated N-stress in nutrient-poor habitats, thereby allowing new (nitrophilic) species to colonise the habitat. This further implies that the putative decline in species number at higher N deposition due to local species loss outweighing increases through new coloniser species has not been reached (yet) in most vegetation classes. This lies in contrast to much of the literature finding an unambiguous negative effect of N deposition on species number (Duprè *et al.*, 2010; Stevens *et al.*, 2010a; Wesche *et al.*, 2012; Roth *et al.*, 2013, Payne *et al.*, 2013; 2015; Storkey *et al.*, 2015), which

here only applies to the MOL class. With much of the directly comparable literature stemming from Swiss grasslands (e.g. Roth *et al.*, 2013, 2015, 2019; Häberlin & Dengler, 2025; Rumpf *et al.*, 2025), possible explanations underpinning this discrepancy may be the higher current N depositions in large areas of Switzerland compared to Austria (EMEP, 2024) as well as this study's use of pre-industrial data long before N deposition significantly increased compared to many of the above studies using resurvey data starting in the 1960s at the earliest. Additionally, this discrepancy may be due to other methodological differences (hard to quantify though they may be), for instance in the seminal work of Stevens *et al.* (2010a) on acidic grasslands of the NAR class in Western Europe, where the selected communities were exceptionally nutrient-poor and therefore likely indeed more sensitive to N.

This study instead adds to the small but nonetheless significant evidence of the variable effects of N deposition on species richness. Opposite to the results of Stevens *et al.* (2010a), evidence from high-elevation NAR communities in the Pyrenees linked N deposition alongside rising temperatures and grazing to increased species richness (Boutin *et al.*, 2017). There, the authors hypothesised that a release from abiotic constraints through warmer temperatures and greater N availability in high-elevation grasslands counterbalance the otherwise negative effects of N deposition on species richness. Diekmann *et al.* (2014), on the other hand, found no effect of N deposition on species richness in calcareous grasslands in Germany, linking this to the higher pH substrate compared to literature on acidic soils. Moreover, Staude *et al.* (2022) showed that eutrophication leads to a gradual exchange of specialist by generalist species while local species numbers stay relatively constant.

The MOL class having the only negative predicted relationship between N deposition and species (-2%) can perhaps be understood as existing nutrient-based competition already occurring here, with MOL being the only meso- to eutrophic vegetation class, such that further N input does not open new colonisation opportunities for nutrophilic species. Humbert *et al.* (2016) indeed showed that managed communities experienced stronger negative effects of N addition, while the research of Stevens *et al.* (2010a) on acidic NAR grasslands found that communities with higher background N depositions were less sensitive to additional depositions, suggesting that more eutrophic grasslands may generally be less sensitive to additional nutrient input. Research on predominantly MOL communities in northern Germany, however, found far greater plot-level reductions in species number between 30–50% over four to five decades compared to the predicted -2% here (Wesche *et al.*, 2012).

The strong positive predicted effect of N deposition on species number for the FEP class (+45%) is likely linked to FEP's small geographic distribution, with plots largely concentrated around Lake Neusiedl. One may speculate that the plots around Lake Neusiedl, which have lower N depositions than the distant FEP plots (Buxbaum *et al.*, 2023), have higher salt concentrations and a more halophytic species profile, therefore being less readily colonised. More distant FEP plots, such as those by the Leitha Mountains, would correspondingly have

lower salt concentrations and higher N depositions, resulting in an increase in species number; this hypothesis is further supported by the small ΔN range FEP occupies and the small negative correlation between ΔN and the mean indicator value for salt (S) across all FEP plots, $r(516) = -0.110$, $p = 0.012$.

4.2.2 Mean N-value and Ratio N ~ ΔN

The positive correlation between ΔN and mean N-value is in line with expectations, signifying a shift towards more nitrophilic species at higher N depositions across all vegetation classes. The Ratio N results mirror this, acting as an alternative measure of nitrophily/eutrophy (Rowe *et al.*, 2016). This relationship is supported by existing literature (e.g. Wesche *et al.*, 2012; Klinkovská *et al.*, 2024, 2025; Rumpf *et al.*, 2025), particularly when using data spanning many decades (*cf.* Roth *et al.*, 2019).

Here, the minimal changes predicted in MOL (+5%) are likely due to the eutrophic to mesotrophic nature of the class making it stable with regard to nutrient-induced species turnover. The more significant shift towards higher N-values in resurveyed MOL communities in Germany found by Wesche *et al.* (2012) demonstrates the difficulty with which our results can be compared with those of resurvey studies. Resurvey studies predominantly examine temporal trends, inferring links between known trends in e.g. deposition rates with observed vegetation changes. Differences in methodology must also be considered when dealing with space-for-time substitution studies (e.g. Stevens *et al.*, 2010a), which use spatial gradients e.g. in deposition to mirror temporal trends. This study can thus be considered a hybrid of the two methodologies, with a spatial gradient given by the spatial spread of plots throughout Austria, while time is an implicit component of the data. Great care must therefore be taken when interpreting our results and comparing them with those of other studies.

Land management of plots was not accounted for in the data as no such data exists at the scale necessary for this study. Obvious interactions with N deposition exist, such as mowing frequency and fertilisation, or with fallows shown to promote N accumulation in the soil (Nielsen & Calderón, 2011; Zeleke, 2017). Especially in the case of FES, which experienced the highest predicted RES for mean N-value, this was a consideration, however without further data, this can at most only be conceptually considered when interpreting the results. Nevertheless, cessation of usage is likely not a major factor in this study as many of the plots were surveyed for phytosociological purposes, meaning that plot locations were generally selected on the basis of being typical for their vegetation class (e.g. not selecting completely fallow areas for FES plots). A further potential confounding factor is the increased solid and liquid manure fertiliser due to agricultural intensification in certain areas that may contribute to high N deposition from the air. Moreover, ammonia being deposited in the form of ammonium only a few hundred metres from its application is very likely not accurately

represented in the larger-scale EMEP data. Specific and detailed land-use management data would be required to address both of these issues more closely.

4.2.3 Mean R-value ~ ΔN

The small but nonetheless significant positive correlation between ΔN and mean-R values is entirely unexpected, as one would expect that the acidifying effects of N depositions should result in a more acidophilic species profile. This unexpected result is mirrored in the positive correlation between mean N- and mean-R values ($r = 0.247$). In fact, resurvey data from mostly calcareous grasslands in the Swiss Alps found increases in soil pH despite N and S depositions (Rumpf *et al.*, 2025), implicating the substrate's pH as a potential factor as well as implying a more complex relationship than simple direct soil acidification through N (and S) deposition.

Interestingly, here, the three vegetation classes whose mean R-values respond most positively to increasing ΔN are LOI, NAR, and SES, which all share similar curve profiles. A possible explanation for this is that temperature has a confounding effect. LOI, NAR, and SES in fact also behave similarly in their response of mean T-value to ΔT. This combined with the moderate correlation between mean T-values and mean R-values ($r = 0.490$) suggest that the observed increase in mean R-values is strongly influenced by ΔT and not just by ΔN. A biological interpretation of this is that at higher temperatures thermophilic species, with a tendency to be basophilic, colonise these vegetation classes, resulting in the observed increase in mean R-values despite the acidifying effects of increased N (which is itself correlated with ΔT). Furthermore, these vegetation classes are alpine or subalpine, and are therefore expected to respond more strongly to increases in temperature (see below). The minimal responses of the remaining vegetation classes support this interpretation, with FES even having a slight negative correlation between mean R-value and ΔN.

4.3 Sulphur depositions

4.3.1 Alpha biodiversity ~ ΔS

The predicted effect of ΔS on species number was minimal overall, with little variation between vegetation classes. Contrary to expectations — that the acidifying effects of S would lead to local species loss (Mitchell *et al.*, 2018; Tipping *et al.*, 2021; Seaton *et al.*, 2023) — all vegetation classes showed slight positive correlations, which can likely be attributed largely to effects arising from correlations between Δs and not due to S itself. The exception to this is FES, whose relatively strong positive correlation between ΔS and species number may be due

to its communities predominantly growing on base-rich soils where acidification through S depositions may allow for new, more acidophilic species to colonise the area more rapidly than native basophilic species are lost. This is partially supported by literature finding base-rich soils to be more resistant to changes through acidification (Diekmann *et al.*, 2014; Storkey *et al.*, 2015). Why the same does not hold true for the calcareous SES class is unclear. Furthermore, the lack of any difference in response between the SES class and the base-poor LOI and NAR classes further suggest that these results are largely due to effects arising from correlations between Δs and not due to S itself.

4.3.2 Mean R-value ~ ΔS

The predicted effect of ΔS on mean R-values is very similar to that of ΔN on mean R-values, with the speculative explanation for the unexpected results being largely the same. Despite baseline S being a moderately important predictor in the mean R-value models (following baseline temperature and vegetation class), there is a lack of strong evidence in the data for ΔS having a strong direct effect on alpha biodiversity or mean R-values. The expected shift towards basophilic species as a result of decreasing S deposition, as reported by Seaton *et al.* (2023) across various types of seminatural grassland habitats in the UK, was definitively not observed here and lack thereof is likely due to more complex interactions between Δs for which data required further analysis is insufficient.

4.4 Temperature changes

4.4.1 Alpha biodiversity ~ ΔT

The effect of ΔT on alpha biodiversity was found to be vegetation class-dependent, such that the overall slight negative correlation does not carry much weight on its own. The strong positive effect of ΔT on species number observed in LOI (+23%) is likely due to the fact that as an alpine class, with there being a general inverse relationship between altitude and temperature (e.g. Körner, 2007), LOI is more sensitive to increases in temperature. Thermophilic species growing at the base of mountains need to cross far shorter distance to colonise LOI communities at higher altitudes than would be the case for non-alpine vegetation classes where thermophilic species have to follow the far more stretched latitudinal lapse rates (De Frenne *et al.*, 2013b), resulting in the high predicted positive effect. Klinkovská *et al.* (2025) argue similarly regarding their results of resurvey data of Czech grasslands between 1971–2023, which predicted an increase in species richness in alpine and subalpine grasslands

across the overall +1.3°C temperature increase across the same period. The other of our selected alpine classes, SES, was predicted to behave otherwise. The predicted negligible effect of ΔT on species number in SES (-2%) may be attributed to its calcareous soil drying out faster at higher temperatures compared to LOI, resulting in minimal change in species number overall because more favourable temperature trades off with negative drought effects. In a resurvey study of calcareous grasslands in the northeastern Austrian Alps from 1999–2013, Gritsch *et al.* (2016) found differing responses between SES-subtypes, with one showing a slight, non-significant decrease in mean species number (matching our results) while the other increased significantly.

Large decreases in species numbers in response to ΔT were predicted for FES and MOL, with losses of ~11.4 and ~8.6 species on average across their ΔT ranges respectively, arguably constituting the most significant responses in this study. In both of these classes species loss may be attributed to drought effects through increased evapotranspiration at higher temperatures i) exceeding the drought tolerance of native FES species and ii) drying out MOL wet meadows, thereby driving hygrophilic species to local extinction (Schwaiger *et al.*, 2022). Surprisingly, previous studies have associated climate warming with increases in species richness in both of these classes (Schwaiger *et al.*, 2022; Klinkovská *et al.*, 2025). Similarly, the predicted negligible effect of ΔT in the NAR class (+1%) was not mirrored by the literature (Boutin *et al.*, 2017; Schwaiger *et al.*, 2022; Klinkovská *et al.*, 2025; Häberlin & Dengler, 2025). Though the reasons for these inconsistencies remain unclear, one potential explanation relates back to the long time series used in this study. Perhaps these vegetation classes' responses to changes in temperature tended to be negative in the first half of the 20th century, a time period which many of the above studies do not account for. This could theoretically be explained through the loss of highly specialised species through temperature increases early on in the 20th century that was not able to be balanced out by the gain of new species; this explanation hinges on those specialists being unable to be 'regained' once lost, such that the temperature-related decrease in species number necessarily occurred toward the beginning of the 20th century.

Lastly, the strong positive correlation observed in FEP has little grounding in the literature, but may in part be explained by interactions between Δs, as well as by the relative increase in species number (+19%) across its ΔT range appearing much more significant than the absolute increase (~+1.8).

4.4.2 Mean T-value ~ ΔT

The overall effect of ΔT on mean T-values was less significant than expected at only +3%, however the subalpine and alpine vegetation classes — NAR, LOI, SES — showed relatively strong predicted effects, in line with expectations. As above these three classes share similar

curve profiles with much lower base mean T-values than the other classes and with the mean T-values only responding positively to ΔT values above ~0.8°C. This implies that the thermic species profile in these habitats at ΔT values < 0.8°C is stable but changes at ΔT values ≥ 0.8°C, as thermophilic species are able to readily migrate up to the higher altitudes whilst native cold-adapted species are lost. This finding is supported by evidence from montane, subalpine, and alpine habitats showing thermophilisation with climate warming (Gritsch *et al.*, 2016; Boutin *et al.*, 2017; Roth *et al.*, 2019; Häberlin & Dengler, 2025). Other studies of such habitats, however, found no significant changes in mean T-values over time, with Rumpf *et al.* (2025) proposing that their results may be due to land-use changes having a greater and confounding effect, while the results of Schwaiger *et al.* only reflect changes since 1995, drawing attention to the potential delay in response of community composition to climate warming (Bertrand *et al.*, 2011; De Frenne *et al.*, 2013a; Lenoir *et al.*, 2013).

The lack of any strong predicted response in our lowland vegetation classes — FEP, FES, MOL — suggests that these classes are more resilient to changes in temperature regarding their species composition – or that impacts need longer to become realised. Once again, there is literature to the contrary, showing thermophilisation over time in FES and MOL communities, suggest that differences in approaches and timeframes may play a significant role (Schwaiger *et al.*, 2022; Klinkovská *et al.*, 2025). Notwithstanding, evidence from a recent Europe-wide study revealed very similar patterns as found here, with alpine and subalpine grasslands showing a significant increase in mean T-values from 1960–2020, while all other grassland types remained stable (Midolo *et al.*, unpublished). Additionally, since changes in land use were not accounted for in our study, the variability among plots we did not account for might be higher in managed grasslands as compared to unmanaged ones. In relation to the aforementioned species loss at higher ΔT values observed in FES and MOL, this suggests that the species losses in FES and MOL are indeed due to moisture effects and not temperature directly.

4.4.3 Mean F-value ~ ΔT

The effect of ΔT on the mean F-values was negligible overall, with the moderate negative effect observed in FES signifying a shift toward xerophilic species at higher temperatures, as otherwise expected. The predicted negative effect of ΔT on mean F-values in FES and the positive effect in FEP may be explained in an analogous manner to the effect of ΔT on species numbers in these classes (see above). There is no consensus across all vegetation classes for the effect of rising temperatures on the mean F-value, with evidence for strongly idiosyncratic responses depending on the habitat (Gritsch *et al.*, 2016; Häberlin & Dengler, 2025; Klinkovská *et al.*, 2024, 2025). The general lack of strong response of mean F-values to increasing temperatures may also be partially explained by elevated atmospheric CO_2

concentrations and warmer temperatures having counteracting effects on evapotranspiration, with plants requiring less evapotranspiration to fix the same amount of carbon at higher atmospheric CO_2 concentrations (Swann *et al.*, 2016; Kirschbaum & McMillan, 2018). The drying effects of climate warming would thus be opposed by the elevated atmospheric CO_2 concentrations such that less drought-adapted species would be able to persist despite drying. Moreover, rising temperatures alone may not drive large changes in humidity conditions in these habitats, with potential of buffering of macroclimatic effects through microclimatic conditions (De Frenne *et al.*, 2013a; Lenoir *et al.*, 2013). This explanation is, however, inconsistent with the hypothesis of drought effects resulting in hygrophilic species loss in MOL wet meadows at higher temperatures (*cf.* Schwaiger *et al.*, 2022), suggesting once again a more complex interplay between variables and existing correlations between them.

4.5 Limitations of this study

This study was able to successfully use combined datasets, though not without some issues. As is generally the case when using data from different studies, differences in methodology and research objectives are often mirrored in differences in the data, and while this is generally unavoidable, the core of this study was fortunately not too strongly impacted by this. The related greater limitation of this study, however, was the general lack of resurvey data. Resurvey data allows for ecological trends to be investigated over long time periods — though not without its own potential challenges (Kapfer *et al.*, 2016; Stuble *et al.*, 2020) — and without which a time component cannot be (directly) included in the analysis. Given the nature of this study, collating various datasets from the last century across all of Austria, the same magnitude of a dataset and breadth of geographic and temporal distribution in the form of resurvey data would be functionally impossible to produce. Moreover, resurvey studies sometimes involve taking detailed vegetation and physio-chemical measurements, such as depositions, of plots at multiple timepoints; here, especially for older plots, deposition measurements were not taken on site at plots, but rather at certain stations across the country, with depositions of intervening areas being interpolated. This is sure to have resulted in more coarse deposition data in this study, which may not necessarily reflect the actual depositions occurring, in particular not accounting for small-scale differences in deposition.

Secondly, the lack of harmonised species abundance data across plots limited the scope of interpretation. Using alpha biodiversity as a measure of diversity is useful in showing absolute increases or decreases in species number, but cannot be used to detect changes in species composition (*cf.* Roth *et al.*, 2015). Ecological indicator values partially address this gap but are themselves subject to criticism, as summarised by Niemi & McDonald (2004). A review by Bartelheimer & Poschlod (2016) on Ellenberg's indicator values, on the other hand, found

that various plant traits can serve as determinants for the different indicator values, suggesting that plant properties occur in syndromes that reflect their indicator values. The authors thus propose that such insights gained may help elucidate the drivers of plants species' ecological niches, highlighting the potential of indicator values. Without abundance data, however, the indicator values cannot be used to calculate community weighted means (CWMs), as a result of which individual vegetation observations of species with outlying indicator values may unduly skew the mean indicator values. This is exacerbated on plots with low species numbers, which may in fact help explain some of the unexpected results of the FEP class, which generally only carries 10–14 species in all of the given models.

Finally, the interpretation of the results was limited by the partially unexplainable correlations between the Δs and between various mean indicator values, coupled with missing precipitation data that may have a confounding effect and as yet unexplored spatial patterns in the data. These factors come together to produce results that defy ecological maxims, namely those regarding mean R-values, warranting further research to disentangle these interactions.

5. Conclusion

The primary objective of this study was to leverage existing data to address a research gap — the effect of nitrogen and to a lesser extent sulphur depositions on grassland communities in Austria. The results showed a clear increase in nitrophilic species at higher N inputs across vegetation classes, with the classes predicted to experience the strongest effects presenting potential targets for conservation efforts. Declining N emissions and depositions in Europe is certainly favourable for conservation of these habitats but will still take many years to take visible effect in the plant composition. Unexpectedly, both N and S depositions were predicted to result in more basophilic species profiles — likely the result of confounding effect of temperature and correlations between variables. The effect of N deposition on species numbers across most vegetation classes showed small-to-moderate positive responses, contrary to much of the existing literature, representing a potential new view on the super long-term effects of N deposition on oligotrophic grassland communities in a country with more moderate N depositions (as compared to e.g. Switzerland). The effects of S deposition on species number were predicted to be minimal overall.

Instead, temperature anomalies were predicted to have a much greater effect on species number, with dry grassland and wet meadows being the most sensitive to increased temperatures, further cementing temperature as one of the single most important climatic

variables for biodiversity (Butterfield & Munson, 2016; Guitar *et al.*, 2016). Temperature was also found to have a profound effect on alpine and subalpine communities, likely by promoting colonisation by thermophilic species and loss of local species, thereby adding to the growing evidence of the threat climate change poses to alpine and subalpine ecosystems (Schwager & Berg, 2019; Inouye, 2020).

Integrating the results of this paper with resurvey vegetation data in order to make substantiated, data-based predictions as to future trends of these communities proves an attractive avenue, especially in light of increasing global temperatures, which themselves have been found to interact with N deposition in driving changes in plant diversity (Humbert *et al.*, 2016; Boutin *et al.*, 2017). Moreover, comparing the knowledge gained here with that of other ecosystem types, notably Austrian forests (Hülber *et al.*, 2008; Jandl *et al.*, 2012; Helm *et al.*, 2017; Dirnböck *et al.*, 2017), will help elucidate the complex ecological interactions that govern how different ecosystems respond to various forms of pollution to allow for more effective countermeasures to be taken.

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Appendix

Table S1: Hyperparameter tuning results of hyperparameter combinations of mtry values 2, 3, 4, 5, 6, 7 (possible number of variables to split at in each node) and min.node.size values 2, 5, 10, 15 (minimum node size for splitting) for models of all six response variables. Root mean square error (RMSE) and R-squared values are given for each hyperparameter combination of each model. The optimal mtry and min.node.size combinations for each model on the basis of the lowest RMSEs are listed first.

Response	mtry	min.node.size	RMSE	R-squared
ALPHA_BIODIVERSITY	2	10	8,17	0,66
MEAN_F	2	10	0,45	0,83
MEAN_N	2	15	0,45	0,71
MEAN_R	2	15	0,33	0,58
RATIO_N	3	15	0,50	0,90
MEAN_T	2	10	0,28	0,97
ALPHA_BIODIVERSITY	2	15	8,17	0,66
MEAN_F	2	5	0,45	0,83
MEAN_N	2	10	0,45	0,71
MEAN_R	3	15	0,33	0,58
RATIO_N	2	10	0,50	0,90
MEAN_T	2	5	0,28	0,97
ALPHA_BIODIVERSITY	2	5	8,19	0,66
MEAN_F	3	10	0,45	0,83
MEAN_N	3	15	0,45	0,71
MEAN_R	2	10	0,33	0,58
RATIO_N	3	10	0,50	0,90
MEAN_T	2	15	0,28	0,97
ALPHA_BIODIVERSITY	3	15	8,20	0,66
MEAN_F	2	2	0,45	0,83
MEAN_N	3	10	0,45	0,71
MEAN_R	4	15	0,33	0,58
RATIO_N	2	15	0,50	0,90
MEAN_T	3	10	0,28	0,97
ALPHA_BIODIVERSITY	3	10	8,20	0,66
MEAN_F	3	15	0,45	0,83
MEAN_N	4	15	0,45	0,71
MEAN_R	5	15	0,34	0,58
RATIO_N	2	5	0,50	0,90
MEAN_T	3	15	0,28	0,97
ALPHA_BIODIVERSITY	4	15	8,22	0,66
MEAN_F	3	5	0,45	0,83
MEAN_N	2	5	0,45	0,71
MEAN_R	3	10	0,34	0,58
RATIO_N	4	15	0,50	0,90
MEAN_T	2	2	0,28	0,97
ALPHA_BIODIVERSITY	2	2	8,22	0,66

MEAN_F	2	15	0,45	0,83
MEAN_N	4	10	0,45	0,71
MEAN_R	6	15	0,34	0,58
RATIO_N	4	10	0,50	0,90
MEAN_T	3	5	0,28	0,97
ALPHA_BIODIVERSITY	3	5	8,23	0,66
MEAN_F	4	10	0,45	0,83
MEAN_N	5	15	0,46	0,71
MEAN_R	4	10	0,34	0,58
RATIO_N	5	15	0,50	0,90
MEAN_T	4	10	0,29	0,97
ALPHA_BIODIVERSITY	4	10	8,23	0,65
MEAN_F	4	15	0,45	0,83
MEAN_N	3	5	0,46	0,71
MEAN_R	5	10	0,34	0,58
RATIO_N	3	5	0,50	0,90
MEAN_T	4	15	0,29	0,97
ALPHA_BIODIVERSITY	5	15	8,26	0,65
MEAN_F	3	2	0,45	0,83
MEAN_N	5	10	0,46	0,71
MEAN_R	7	15	0,34	0,58
RATIO_N	5	10	0,50	0,90
MEAN_T	3	2	0,29	0,97
ALPHA_BIODIVERSITY	3	2	8,27	0,65
MEAN_F	4	5	0,45	0,83
MEAN_N	6	15	0,46	0,71
MEAN_R	2	5	0,34	0,58
RATIO_N	2	2	0,50	0,90
MEAN_T	4	5	0,29	0,97
ALPHA_BIODIVERSITY	5	10	8,27	0,65
MEAN_F	5	10	0,45	0,83
MEAN_N	2	2	0,46	0,71
MEAN_R	6	10	0,34	0,58
RATIO_N	4	5	0,51	0,90
MEAN_T	5	10	0,29	0,97
ALPHA_BIODIVERSITY	4	5	8,27	0,65
MEAN_F	5	15	0,45	0,83
MEAN_N	4	5	0,46	0,71
MEAN_R	3	5	0,34	0,57
RATIO_N	6	15	0,51	0,90
MEAN_T	5	15	0,29	0,97
ALPHA_BIODIVERSITY	6	15	8,27	0,65
MEAN_F	5	5	0,45	0,83
MEAN_N	6	10	0,46	0,71
MEAN_R	7	10	0,34	0,57
RATIO_N	3	2	0,51	0,90

MEAN_T	4	2	0,29	0,97
ALPHA_BIODIVERSITY	6	10	8,29	0,65
MEAN_F	4	2	0,45	0,83
MEAN_N	7	15	0,46	0,71
MEAN_R	4	5	0,34	0,57
RATIO_N	6	10	0,51	0,90
MEAN_T	5	5	0,29	0,97
ALPHA_BIODIVERSITY	7	15	8,29	0,65
MEAN_F	6	10	0,45	0,83
MEAN_N	3	2	0,46	0,70
MEAN_R	2	2	0,34	0,57
RATIO_N	5	5	0,51	0,90
MEAN_T	6	10	0,29	0,97
ALPHA_BIODIVERSITY	5	5	8,30	0,65
MEAN_F	6	15	0,45	0,83
MEAN_N	5	5	0,46	0,70
MEAN_R	5	5	0,34	0,57
RATIO_N	4	2	0,51	0,90
MEAN_T	6	15	0,29	0,97
ALPHA_BIODIVERSITY	4	2	8,30	0,65
MEAN_F	5	2	0,45	0,83
MEAN_N	7	10	0,46	0,70
MEAN_R	3	2	0,34	0,57
RATIO_N	7	15	0,51	0,90
MEAN_T	5	2	0,29	0,97
ALPHA_BIODIVERSITY	7	10	8,31	0,65
MEAN_F	6	5	0,45	0,83
MEAN_N	4	2	0,46	0,70
MEAN_R	6	5	0,34	0,57
RATIO_N	6	5	0,51	0,90
MEAN_T	6	5	0,29	0,97
ALPHA_BIODIVERSITY	8	15	8,31	0,65
MEAN_F	7	10	0,45	0,83
MEAN_N	6	5	0,46	0,70
MEAN_R	7	5	0,34	0,57
RATIO_N	5	2	0,51	0,90
MEAN_T	7	10	0,29	0,97
ALPHA_BIODIVERSITY	6	5	8,32	0,65
MEAN_F	7	15	0,45	0,83
MEAN_N	5	2	0,46	0,70
MEAN_R	4	2	0,34	0,57
RATIO_N	7	10	0,51	0,90
MEAN_T	7	15	0,29	0,97
ALPHA_BIODIVERSITY	8	10	8,33	0,65
MEAN_F	7	5	0,45	0,83
MEAN_N	7	5	0,46	0,70

MEAN_R	5	2	0,34	0,57
RATIO_N	6	2	0,51	0,90
MEAN_T	6	2	0,29	0,97
ALPHA_BIODIVERSITY	5	2	8,33	0,65
MEAN_F	6	2	0,45	0,83
MEAN_N	6	2	0,46	0,70
MEAN_R	6	2	0,34	0,56
RATIO_N	7	5	0,51	0,90
MEAN_T	7	5	0,29	0,97
ALPHA_BIODIVERSITY	7	5	8,35	0,64
MEAN_F	7	2	0,46	0,83
MEAN_N	7	2	0,46	0,70
MEAN_R	7	2	0,34	0,56
RATIO_N	7	2	0,52	0,90
MEAN_T	7	2	0,29	0,97
ALPHA_BIODIVERSITY	6	2	8,36	0,64
ALPHA_BIODIVERSITY	8	5	8,37	0,64
ALPHA_BIODIVERSITY	7	2	8,38	0,64
ALPHA_BIODIVERSITY	8	2	8,39	0,64

Table S2: Summary statistics for all six response variables' models using their optimal hyperparameter combinations (Table S1). For each model the importance scores for each of the model's predictors are given. For each model the R-squared value, root mean square error (RMSE), and standard deviation (SD) are given.

Response	Predictor	Importance	R-squared	RMSE	SD
ALPHA_BIODIVERSITY	BASELINE_TEMP	95,05	0,66	8,16	14,03
ALPHA_BIODIVERSITY	SURF_AREA	88,12	0,66	8,16	14,03
ALPHA_BIODIVERSITY	BASELINE_N	86,23	0,66	8,16	14,03
ALPHA_BIODIVERSITY	BASELINE_SOX	78,51	0,66	8,16	14,03
ALPHA_BIODIVERSITY	VEG_CLASS	76,76	0,66	8,16	14,03
ALPHA_BIODIVERSITY	DELTA_N	64,45	0,66	8,16	14,03
ALPHA_BIODIVERSITY	DELTA_SOX	62,93	0,66	8,16	14,03
ALPHA_BIODIVERSITY	DELTA_TEMP	62,28	0,66	8,16	14,03
MEAN_F	VEGE_CLASS	1,60	0,83	0,45	1,10
MEAN_F	BASELINE_TEMP	0,84	0,83	0,45	1,10
MEAN_F	BASELINE_SOX	0,51	0,83	0,45	1,10
MEAN_F	BASELINE_N	0,43	0,83	0,45	1,10
MEAN_F	DELTA_N	0,37	0,83	0,45	1,10
MEAN_F	DELTA_TEMP	0,29	0,83	0,45	1,10
MEAN_F	DELTA_SOX	0,27	0,83	0,45	1,10
MEAN_N	BASELINE_TEMP	0,62	0,71	0,45	0,84
MEAN_N	VEGE_CLASS	0,35	0,71	0,45	0,84
MEAN_N	BASELINE_SOX	0,35	0,71	0,45	0,84
MEAN_N	DELTA_N	0,31	0,71	0,45	0,84

MEAN_N	BASELINE_N	0,29	0,71	0,45	0,84
MEAN_N	DELTA_TEMP	0,28	0,71	0,45	0,84
MEAN_N	DELTA_SOX	0,23	0,71	0,45	0,84
MEAN_R	VEGE_CLASS	2,15	0,90	0,50	1,61
MEAN_R	BASELINE_TEMP	1,56	0,90	0,50	1,61
MEAN_R	BASELINE_SOX	0,93	0,90	0,50	1,61
MEAN_R	BASELINE_N	0,62	0,90	0,50	1,61
MEAN_R	DELTA_SOX	0,61	0,90	0,50	1,61
MEAN_R	DELTA_N	0,59	0,90	0,50	1,61
MEAN_R	DELTA_TEMP	0,35	0,90	0,50	1,61
MEAN_T	BASELINE_TEMP	2,57	0,97	0,28	1,72
MEAN_T	VEGE_CLASS	1,25	0,97	0,28	1,72
MEAN_T	BASELINE_SOX	0,26	0,97	0,28	1,72
MEAN_T	BASELINE_N	0,24	0,97	0,28	1,72
MEAN_T	DELTA_N	0,24	0,97	0,28	1,72
MEAN_T	DELTA_TEMP	0,15	0,97	0,28	1,72
MEAN_T	DELTA_SOX	0,14	0,97	0,28	1,72
RATIO_N	BASELINE_TEMP	0,21	0,58	0,33	0,52
RATIO_N	VEGE_CLASS	0,17	0,58	0,33	0,52
RATIO_N	BASELINE_SOX	0,13	0,58	0,33	0,52
RATIO_N	DELTA_N	0,11	0,58	0,33	0,52
RATIO_N	BASELINE_N	0,10	0,58	0,33	0,52
RATIO_N	DELTA_TEMP	0,10	0,58	0,33	0,52
RATIO_N	DELTA_SOX	0,09	0,58	0,33	0,52

Table S3: Pearson's correlation coefficients (*r*), degrees of freedom, and *p*-values respectively between pairs of predictor Δs across all vegetation survey plots, divided by vegetation class and overall.

	r						
Predictors	***FES***	***FEP***	***MOL***	***NAR***	***LOI***	***SES***	***Total***
ΔN - ΔS	0,55; 5489; < 0.001	0,628; 516; < 0.001	0,198; 783; < 0.001	0,51; 1889; < 0.001	0,792; 2048; < 0.001	0,613; 3805; < 0.001	0,509; 14540; < 0.001
ΔN - ΔT	0,176; 5489; < 0.001	0,462; 516; < 0.001	0,577; 783; < 0.001	0,202; 1889; < 0.001	0,283; 2048; < 0.001	0,235; 3805; < 0.001	0,302; 14540; < 0.001
ΔT - ΔS	-0,572; 5489; < 0.001	-0,373; 516; < 0.001	-0,427; 783; < 0.001	-0,468; 1889; < 0.001	-0,036; 2048; < 0.001	-0,251; 3805; < 0.001	-0,394; 14540; < 0.001

Table S4: Pearson's correlation coefficients (*r*), degrees of freedom (df), and *p*-values (p) between pairs of ecological indicator values across all vegetation survey plots.

Variable pair	***r***	***df***	***p***
Mean T - Mean F	-0,313	14533	< 0.001
Mean T - Mean R	0,490	14539	< 0.001
Mean T - Mean N	0,461	14539	< 0.001
Mean F - Mean R	-0,355	14534	< 0.001
Mean F - Mean N	0,420	14534	< 0.001
Mean R - Mean N	0,247	14540	< 0.001