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Atmospheric Nitrogen Deposition to Global Forests

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# Responses of forest ecosystems in Europe to decreasing nitrogen deposition

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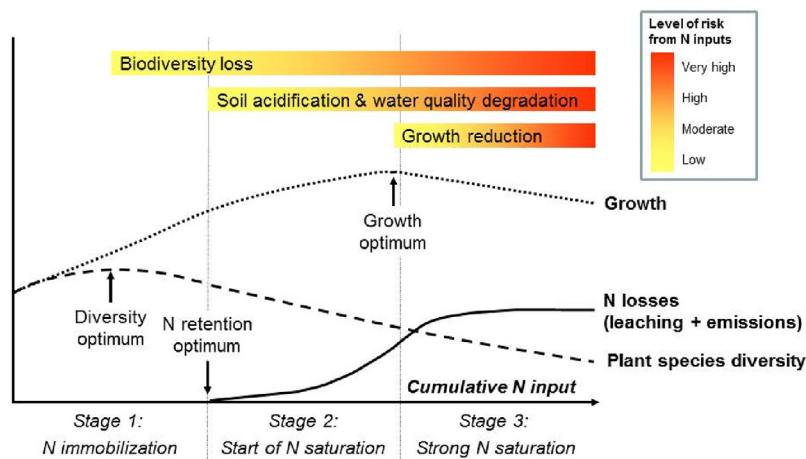
## 1. Introduction

Anthropogenic emissions drastically altered the global nitrogen (N) cycle (Fowler et al., 2013; Galloway et al., 2003; Vitousek et al., 1997), with human activities becoming the dominant contribution to the annual release of reactive N to the atmosphere (Fowler et al., 2015; Galloway et al., 2004). The increase in anthropogenic emissions arose from accelerated fossil fuel burning since the industrial revolution, the advent of the Haber-Bosch process to create reactive N from inert atmospheric N<sub>2</sub> at the start of the 20th century as well as an increase in mass transportation and livestock numbers (Engardt et al., 2017; Erisman et al., 2011). Today, 18% of the global anthropogenic N fixation can be attributed to combustion processes, 55% to fertilizer production, and 27% to biological N fixation in agriculture (Fowler et al., 2015). These activities have created benefits, such as the support of human nutrition by mineral fertilizers (Erisman et al., 2008). On the other hand, the release of reactive N causes considerable damages to human health (Van Grinsven et al., 2013) and induces changes in natural and seminatural ecosystems, such as N deposition being one of the greatest threats to global plant diversity (Bobbink et al., 2010; Brink et al., 2011; Clark et al., 2013; Erisman et al., 2008; Soons et al., 2017; Vitousek et al., 1997).

In Europe N emissions and corresponding deposition increased from preindustrial times till the mid-1980s, followed by a decrease since the 1990s (Engardt et al., 2017). The decline in N emissions is due to a combination of

emission abatement policies and economic transformation (Erisman et al., 2003). In Europe's forests, N deposition caused a variety of changes, including impacts on tree productivity (De Vries et al., 2006, 2017b; Kahle, 2008), tree nutrition reflected in foliar nutrient concentrations (Jonard et al., 2015; Sardans et al., 2016b; Waldner et al., 2015), sensitivity of trees to biotic and abiotic stress (Bobbink and Hettelingh, 2011), the composition of understory vegetation (Dirnböck et al., 2014; van Dobben and De Vries, 2017) and ectomycorrhizal fungal communities (van der Linde et al., 2018), to soil chemistry, and increased leaching of N from forest soils to surface and ground waters (Dise et al., 2009; Gundersen et al., 2006). In recent decades, much discussion took place to identify the mechanisms as well as the time frame by which forest ecosystems are impacted by elevated N deposition. The concept of *N saturation* (Aber et al., 1989, 1998; Ågren and Bosatta, 1988; De Vries and Schulte-Uebbing, 2019; Lovett and Goodale, 2011) suggests a set of reactions including loss of plant species diversity, N losses with seepage water, soil acidification, and growth reduction. A recent perspective on the stages of N saturation is depicted in Fig. 13.1. Ecological understanding is used to determine critical loads of N deposition defined as “a quantitative estimate of an exposure to one or more pollutants below which significant harmful effects on specified sensitive elements of the environment do not occur according to present knowledge” (Nilsson and Grennfelt, 1988). Critical loads underpin emission protocols at the European scale such as the

FIG. 13.1 Hypothetical relationship between the stage of N saturation and the effects on terrestrial ecosystems in terms of soil processes, vegetation changes and growth. It illustrates the trade-off between the initial positive impact of nitrogen enrichment on tree growth and related carbon sequestration on the one hand and the negative impact on ecosystem services (e.g., water quality regulation by nitrogen retention) and on biodiversity on the other hand. This figure is adapted from De Vries and Schulte-Uebbing (2019), being an update of the figure by Aber et al. (1998). The figure is reused with permission.



Revised National Emissions Ceilings Directive (NECD) and are also applied for example in North America (Pardo et al., 2011; Schindler and Lee, 2010) and Asia (Duan et al., 2016). Exceedances of critical loads indicate risks of adverse effects on various aspects of forests, such as tree nutrition and forest biodiversity (De Vries et al., 2015; Nordin et al., 2005; Waldner et al., 2015).

A large part of the ecological research in this context focused on the responses of forest ecosystems to elevated N deposition resulting in N saturation or the exceedance of critical loads. However, much less attention was paid to the potential dynamics of a “recovery” from high N loads although a decline of N deposition to Europe can be observed since the 1990s. The average deposition of inorganic N across all land-use types in Europe decreased from  $10.3 \text{ kg N ha}^{-1} \text{ a}^{-1}$  in 1990 to  $6.6 \text{ kg N ha}^{-1} \text{ a}^{-1}$  in 2018 (after Engardt et al. (2017), data kindly provided by Magnus Engardt and David Simpson). The trends are distributed heterogeneously in space. While many forests in areas with higher absolute levels of N deposition (e.g., in Central and Western Europe) experienced a decrease in N inputs, less clear trends have been reported for Northern Scandinavia and parts of Southern Europe (Figs. 13.2 and 13.3). Note that despite these reductions, 62% of the European ecosystem area was at risk of eutrophication in 2015 due to the exceedance of the critical load for eutrophication (Slootweg et al., 2015).

This chapter addresses the response of European forest ecosystems to decreasing N deposition. We review published results from observational and experimental studies on well-monitored parameters: Soil acidification and eutrophication, foliar chemistry, ground vegetation composition, tree vitality, and tree growth. This set of indicators covers a range between *endpoint metrics*, i.e., aspects of the environment that are directly relevant to people (e.g., tree growth) and *midpoint metrics*, i.e., parameters

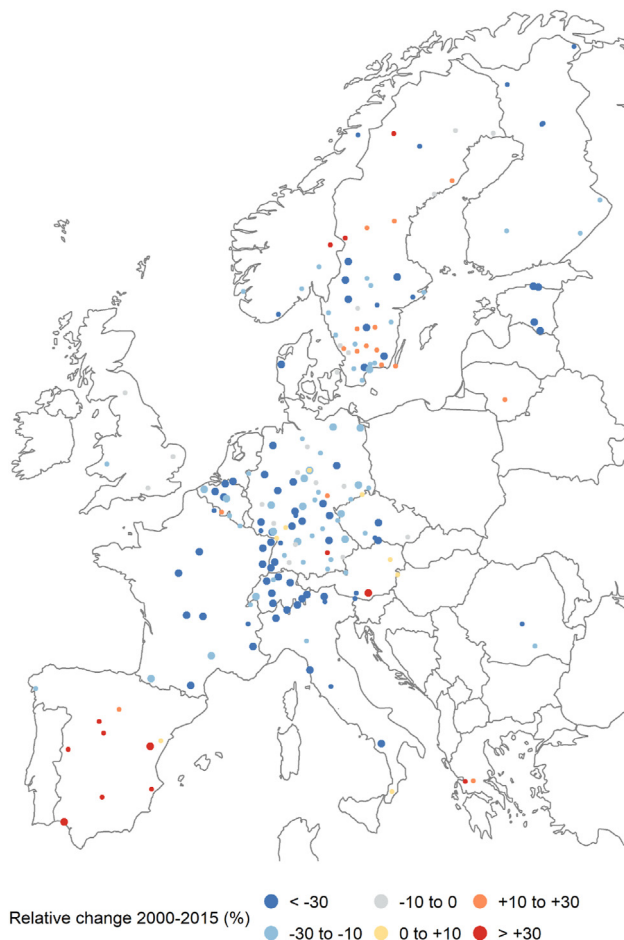
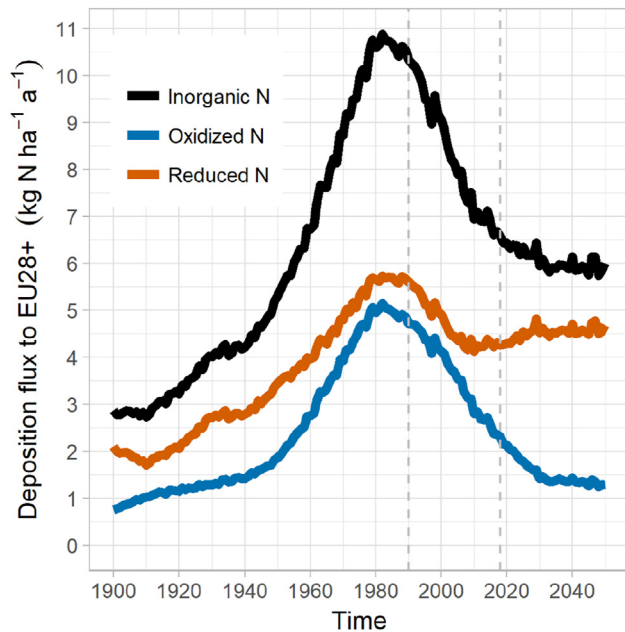


FIG. 13.2 Relative change of throughfall deposition of inorganic N at the intensive monitoring sites of the UNECE ICP forests program network between 2000 and 2015 (redrawn after Schmitz et al., 2018). Large dots indicate statistically significant trends; trends represented by small dots are not statistically significant.



**FIG. 13.3** Average deposition of oxidized, reduced and total N between 1900 and 2050 to the EU28, Norway and Switzerland according to EMEP model results (after Engardt et al. (2017), data kindly provided by Magnuz Engardt and David Simpson). Vertical dashed lines indicate the years 1990 and 2018. Future reductions are expected to be small and inorganic N deposition is likely converging to a level approximately twice as high compared to 1900.

that are well-suited to measure progress toward desired environmental states (e.g., plant tissue concentrations) (Rowe et al., 2017). While results are limited to Europe, references have also been included relating to observations and experiments in the United States (US). For a detailed overview of impacts of decreased N deposition in the US, we refer to (Gilliam et al., 2019, 2023).

## 2. Soil acidification and eutrophication

Atmospheric deposition of reactive N compounds such as nitrate ( $\text{NO}_3^-$ ) and ammonium ( $\text{NH}_4^+$ ) contributes to acidification and eutrophication of forest soils (Driscoll et al., 2006). Soil acidification involves accelerated losses of mineral nutrients (base cations, i.e.,  $\text{Ca}^{2+}$ ,  $\text{K}^+$  and  $\text{Mg}^{2+}$ ) and potential for the mobilization of toxic aluminum (Al), both of which can compromise tree health (Driscoll et al., 2006; Boudot et al., 1994; De Vries et al., 2014; De Wit et al., 2010; Cecchini et al., 2019). N deposition contributes to elevated soil solution  $\text{NO}_3^-$  concentrations and soil N stocks (Driscoll et al., 2001; Wessel et al., 2021). This enrichment can have a variety of effects on trees and ground vegetation, covered in the other chapters of the volume.  $\text{NO}_3^-$  concentrations in soil solution are a good indicator for the soil N status. Important determinants of  $\text{NO}_3^-$  leaching are the C/N ratio of the forest floor

(Gundersen et al., 1998a) and N deposition rates (Dise and Wright, 1995), as well as a variety of other site and stand characteristics controlling the ecosystem N cycling (Lovett and Goodale, 2011). Generally, elevated  $\text{NO}_3^-$  concentrations in soil solution are an indication of N availability in excess of biotic demand. Spatial patterns of soil solution  $\text{NO}_3^-$  are highly variable but partly reflect spatial patterns in N deposition, with higher levels in the Netherlands, Belgium, parts of Germany, Switzerland, Northern Italy and Denmark and lower levels in parts of France, Norway, Northern Sweden, and Finland (Balestrini et al., 2019; Boxman et al., 2008; Braun et al., 2020; De Vries et al., 2007; Evans et al., 2001; Gundersen et al., 1998a; Jonard et al., 2012; Mellert et al., 2008; Moffat et al., 2002; Pannatier et al., 2011; Pihl Karlsson et al., 2011; Rothe et al., 2002; Ukonmaanaho et al., 2014; van der Heijden et al., 2011; Verstraeten et al., 2012). There are relatively fewer reports of elevated  $\text{NO}_3^-$  in soil solution in Southern and Eastern Europe, and N deposition is mostly lower in these regions (Waldner et al., 2014).

## 2.1 Observational studies

At the European scale, studies examining trends in soil solution N show weak or nonsignificant trends. For example, Johnson et al. (2018) found a weakly significant ( $P < .1$ ) reduction in  $\text{NO}_3^-$  concentrations at 40–80 cm depth corresponding to a decrease of 30% over 10 years when analyzing data from 162 plots across Europe between 1995 and 2012. They found no significant trend in 10–20 cm depth. An earlier analysis (from the early 1990s to 2006) using a similar dataset found mostly nonsignificant trends in soil solution inorganic N concentrations (Iost et al., 2012). On the other hand, decreasing trends of inorganic N in runoff water were found to be more common than increasing trends at 17 plots across Europe between 1990 and 2017 (Forsius et al., 2021). These studies did not focus specifically on areas with high N deposition and included many sites from N limited areas of Northern Europe. Within Europe, national and regional studies show variable results. For example, in the Netherlands, Flanders, Northern Italy and Switzerland soil solution  $\text{NO}_3^-$  declined in response to decreasing N deposition (Balestrini et al., 2019; Boxman et al., 2008; Braun et al., 2020; Verstraeten et al., 2012). In contrast, an intensive study at the site Solling in Germany found  $\text{NO}_3^-$  continued leaching from a spruce (*Picea abies*) stand and increased at a beech (*Fagus sylvatica*) stand despite decreasing N deposition between 1973 and 2013, indicating a reduction of the N retention capacity of the soil over time (Meeseburg et al., 2016). Other studies found no trends in  $\text{NO}_3^-$  soil solution concentrations during periods of stable N deposition (e.g., Alewell et al., 2000; Johnson et al., 2013; Pannatier et al., 2011). At heavily acidified forests in the Czech



Republic,  $\text{NO}_3^-$  concentrations in soil solution and inorganic N stream export declined despite no decrease in N deposition. This was due to an increase in N uptake by vegetation and changes in organic matter cycling as the soil became less acidic, related to decreasing S deposition (Oulehle et al., 2011; Švik et al., 2020).

Where soil solution  $\text{NO}_3^-$  decreased, it is often accompanied by a decrease in base cations and total Al concentrations, while soil solution pH and acid neutralizing capacity (ANC) showed no uniform trends in recent decades (Iost et al., 2012; Johnson et al., 2018). Recovery from acidification primarily occurs on poorly buffered, acidic soils while acidification progresses on better buffered soils despite large decreases in sulfur (S), and to a lesser degree, N deposition (Johnson et al., 2018). The absence of a uniform recovery of soil solution from acidification agrees with trends in bulk soil chemistry. Cools and De Vos (2011) found that base saturation increased in soils with low buffering capacity but decreased in soils with initially higher base saturation across Europe. A similar result was found for the Netherlands between 1990 and 2015 (De Vries et al., 2017a). Table 13.1 summarizes results on trends of soil solution eutrophication and acidification status from studies across Europe.

## 2.2 Experimental studies

In addition to observational studies, field experiments also provide information on changes of the soil chemical status under decreasing N deposition. In this context, the NITREX and EXMAN N manipulation experiments at several sites in Europe are a valuable source of information (Wright and Rasmussen, 1998). At three NITREX sites, throughfall N deposition was decreased from 36–50  $\text{kg N ha}^{-1} \text{a}^{-1}$  to 5–16  $\text{kg N ha}^{-1} \text{a}^{-1}$  by roofing. A decline in N leaching became apparent within the first 3 years of treatment at all three sites (Beier et al., 1998; Boxman et al., 1998; Emmett et al., 1998; Gundersen et al., 1998b). A similarly fast response in N leaching has been observed from a roofing experiment in southern Norway (Wright et al., 1993). These results indicate that continuous high N inputs are required to sustain N leaching in most forest ecosystems, suggesting that decreasing deposition quickly translates into improvements in soil water quality (Emmett et al., 1998). This, however, also implies that considerable amounts of N deposited over the last decades are retained and that the return of the ecosystem to the original N status is potentially slow (Gundersen et al., 1998b). In contrast to these findings, also unchanged or increased N leaching despite decreased deposition was occasionally reported from observational (Meeseburg et al., 2016) and experimental studies (Emmett et al., 1998).

## 2.3 Summary

Long-term monitoring data provides information on  $\text{NO}_3^-$  concentrations in soil solution as an indicator for the soil N status. Despite considerable heterogeneity, indications for a decreasing trend in soil solution  $\text{NO}_3^-$  concentrations at the European scale exist. Experimental studies tend to report a faster and more pronounced reaction of soil solution  $\text{NO}_3^-$  concentrations compared to the findings from large-scale observational studies. In the experiments the magnitude and speed of decrease in N supply was larger compared to trends in N deposition in most parts of Europe. Furthermore, longer-term changes in soil microbial activity (e.g., mineralization rates) might be reflected to a larger degree in the observational studies compared to experimental studies which often focus on the time period immediately after the onset of the artificial decrease of N supply. Nevertheless, both types of studies suggest indications of a response in soil solution  $\text{NO}_3^-$  concentrations to decreases in N deposition. Soil acidification shows nonuniform tendencies across Europe despite large-scale decreases in N, and especially S, deposition.

## 3. Understory vegetation

Forests provide habitat for understory vegetation, bryophytes, lichens as well as microbial and animal communities. While N is a limiting resource for many organisms (Vitousek and Howarth, 1991), the efficiency with which it is used is species-specific (Chapin, 1980). As a consequence, more N causes some species to thrive on the expense of others, usually causing a net loss in species diversity (Suding et al., 2005). Besides this effect on interspecific competition, changes in N deposition can also modify herbivory, interactions with fungi, and invasibility by exotic species, thereby affecting understory species composition (Gilliam, 2006). In managed forests these mechanisms are rarely reflected in the composition of the main tree species for they are typically intentionally chosen by forest managers. In contrast, forest understory vegetation, bryophytes, lichens, mycorrhiza, and soil fauna can be expected to be affected by N availability in addition to other environmental factors such as light availability, temperature, moisture, and nutrients other than N. The responses of these groups to elevated N deposition encompass changes in the abundance of species, alteration in the identity of species (species composition), and pauperization of local and regional species diversity (Bobbink et al., 2010; Farrer and Suding, 2016; Hautier et al., 2009; Nijssen et al., 2017). Fig. 13.4 exemplifies effects of N deposition for lichen diversity.

**TABLE 13.1** Summary of trends in soil solution chemical characteristics indicative for eutrophication and acidification status (concentration of  $\text{NO}_3^-$ , base cations (BC, i.e.,  $\text{Ca}^{2+}$ ,  $\text{K}^+$  and  $\text{Mg}^{2+}$ ) and total aluminum ( $\text{Al}_{\text{tot}}$ ), pH, equivalent ratio of BC and  $\text{Al}_{\text{tot}}$  (BC: $\text{Al}_{\text{tot}}$ ), acid-neutralizing capacity (ANC) and ionic strength) from studies across Europe. Arrows indicate the direction of the trend (increase, mixed/complex results with a tendency for increase, no trend, mixed/complex results with a tendency for decrease, decrease).

Effect	Trend				
	↑	↑/↔	↔	↔/↓	↓
$\text{NO}_3^-$		Meesenburg et al. (2016) (Germany)	Johnson et al. (2013) (Ireland), Löfgren and Zetterberg (2011), Pihl Karlsson et al. (2011) (Sweden), Vanguelova et al. (2010) (UK)	Pannatier et al. (2011) (Switzerland), Sawicka et al. (2016) (UK), Ukonmaanaho et al. (2014) (Finland)	Boxman et al. (2008) (Netherlands), Oulehle et al. (2011) (Czech Republic), Verstraeten et al. (2012), Jonard et al. (2012) (Wallonia), Verstraeten et al. (2017) (Flanders), Balestrini et al. (2019) (Italy), Braun et al. (2020) (Switzerland)
pH	Akselsson et al. (2013), Löfgren et al. (2011) (Sweden), Verstraeten et al. (2016) (Flanders)	Vanguelova et al. (2010), Sawicka et al. (2016) (UK), Fölster et al. (2003), Löfgren and Zetterberg (2011), Pihl Karlsson et al. (2011) (Sweden), Johnson et al. (2013) (Ireland)			Boxman et al. (2008) (Netherlands), Jonard et al. (2012) (Wallonia)
BC			Vanguelova et al. (2010) (UK), Johnson et al. (2013) (Ireland)	Pannatier et al. (2011) (Switzerland), Sawicka et al. (2016) (UK), Cecchini et al. (2019) (Italy)	Jonard et al. (2012) (Wallonia), Verstraeten et al. (2012) (Flanders), Boxman et al. (2008) (Netherlands), Fölster et al. (2003), Akselsson et al. (2013) (Sweden)
$\text{Al}_{\text{tot}}$	Jonard et al. (2012) (Wallonia), Fölster et al. (2003) (Sweden)		Sawicka et al. (2016) (UK)	Vanguelova et al. (2010), Löfgren et al. (2011), Löfgren and Zetterberg (2011), Pihl Karlsson et al. (2011) (Sweden), Johnson et al. (2013) (Ireland)	Verstraeten et al. (2012) (Flanders), Boxman et al. (2008) (Netherlands)
BC: $\text{Al}_{\text{tot}}$		Meesenburg et al. (2016) (Germany)		Pannatier et al. (2011) (Switzerland)	Verstraeten et al. (2012) (Flanders), Braun et al. (2020) (Switzerland)
ANC	Akselsson et al. (2013), Löfgren et al. (2011) (Sweden), Verstraeten et al. (2012) (Flanders)	Fölster et al. (2003), Löfgren and Zetterberg (2011), Pihl Karlsson et al. (2011) (Sweden)			
Ionic strength				Löfgren and Zetterberg (2011) (Sweden)	Löfgren et al. (2011) (Sweden), Verstraeten et al. (2012) (Flanders), Vanguelova et al. (2010) (UK)

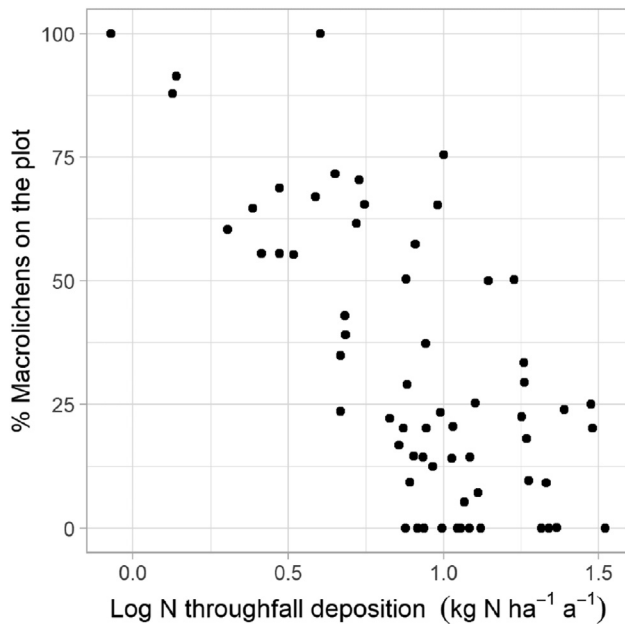


FIG. 13.4 Examples for the effects of N deposition on lichen diversity (proportion of macrolichen species among all lichen species) based on 83 forest plots across Europe. Reused from *Giordani et al. (2014)* with permission.

### 3.1 Observational studies

While there are several observational studies on the reaction of forest understory diversity to elevated N deposition, to our knowledge, none of them focused specifically on the response to declining N deposition. These studies confirm an increase in nitrophilic forest understory plant species on the expense of oligotrophic species both in European-wide (*Dirnböck et al., 2014; van Dobben and De Vries, 2017*) as well as regional contexts (*Bobbink and Hettelingh, 2011; Heinrichs and Schmidt, 2016; Keith et al., 2009; Roth et al., 2015*). Besides N deposition, litter quality, light availability, density of large herbivores, and differences in forest management were also important drivers of change in understory plant communities (*Bernhardt-Römermann et al., 2015; Perring et al., 2017; Verheyen et al., 2012*). These changes in species composition do not, however, seem to be accompanied by a broad scale, synchronized decline in plant diversity in European forests (*Dirnböck et al., 2014; van Dobben and De Vries, 2017; Verheyen et al., 2012*).

In contrast, elevated N deposition has clearly contributed to a dramatic diversity loss in epiphytic lichens in many European forests (*Bobbink and Hettelingh, 2011; Giordani et al., 2014; Hauck et al., 2013; Mayer et al., 2013*). Similarly, major impacts in the community composition and diversity of mycorrhiza were identified at the European level (*Suz et al., 2014; van der Linde et al., 2018*) and in various regional studies (*Bobbink and Hettelingh, 2011, references therein*). Furthermore, diversity

effects of N deposition on one receptor can indirectly affect others such as soil fauna and mammals because effects cascade from e.g., plants to animal species (*Nijssen et al., 2017*) or from soil microbes to plants (*Farrer and Suding, 2016*). However, studies detailing the link between N deposition and animal diversity in Europe's forests are scarce, partly due to the complex dynamics of animal populations and corresponding food-webs (*Nijssen et al., 2017*).

### 3.2 Experimental studies

In addition to these findings from observational studies, a limited number of N manipulation experiments report on changes in understory vegetation in response to decreasing N input. *Strengbom et al. (2001)* compared vascular plant, fungi, and bryophyte communities between control and treatment plots at two experimental forest sites in Sweden where N fertilization was canceled nine and 47 years prior to the analyses, respectively. They found differences in the vascular plant community at the site where treatment ended 9 years ago but no longer at the site where treatment was canceled 47 years ago. Nevertheless, the fungi and bryophyte communities deviated from the control plots at both sites. *Sujetovienė and Stakėnas (2007)* report on changes in pine forest understory plant community in response to drastic emission reductions from a close-by fertilizer plant in Lithuania. They found a decrease in nitrophilous species within the 16 years between two ground vegetation studies (1988 and 2004). It should be noted that also the light conditions and the acidity status of the respective forest stands changed over the same time. In one of the NITREX experiments, N-indicating fern cover significantly decreased after 5 years of reduction of N deposition from 60 to 5 kg N ha<sup>-1</sup> a<sup>-1</sup> by roofing. A recovery of other species was not recorded (*Boxman et al., 1998*).

Findings from grassland vegetation experiments might also be informative for the question of forest understory vegetation response to decreasing N deposition. *Stevens et al. (2012)* found significant differences in Ellenberg N values between control and treatment plots 15 years after cessation of N fertilization in mesotrophic grassland in the UK. *Shi et al. (2014)* report on the vegetation composition 3 years after cessation of N fertilization at a sandy grassland site in Northeast China. They found that the vegetation at the control and the formerly treated plots still differed although indications for an ongoing process of recovery were apparent. *Storkey et al. (2015)* report that grassland biodiversity largely recovered over a period of 20 years of decreasing ambient N deposition, based on observations from the control plot of a fertilization experiment in the UK. The pronounced recovery was potentially supported by the regular export of N from the ecosystem by haying (*Tilman and Isbell, 2015*).

### 3.3 Summary

Recent studies based on large-scale monitoring data find shifts in understory community composition in response to high levels of N deposition but do not report on responses to decreasing N deposition. Results from experimental studies suggest that while the recovery of understory vegetation from high N inputs is possible, time-lags in the order of decades are to be expected. One mechanism causing these delays is that in regions where high N deposition eradicated source populations, back-colonization will be particularly difficult (Clark and Tilman, 2010; Dullinger et al., 2015). The complex consequences of such effects have already been shown for land management legacies' impact on dispersal dynamics and subsequent community alterations (e.g., Burton et al., 2011). Strong recovery delay due to dispersal limitation can be expected for epiphytic lichens because regional species extinctions were particularly pronounced (Hauck et al., 2013). We hypothesize that this delay in the response of understory vegetation to decreases in N deposition partly explains the absence of corresponding trends in Europe-scale observational studies. In addition, changes in other environmental conditions like light availability, forest management, sulfur deposition, habitat loss and fragmentation, climate impact, and nonnative species invasion (see e.g., Perring et al., 2017) superimpose on the signal of N deposition in forest understory communities.

## 4. Tree nutrition

Foliar element concentrations and their ratios reflect the nutritional status of trees. Unbalanced N:P ratios in foliar tissues are frequently associated with defoliation (Bontemps et al., 2011; Ferretti et al., 2015; Veresoglou et al., 2014; Waldner et al., 2015) and an increasing risk of attacks by parasites (Flückiger and Braun, 1998) and herbivores (Pöyry et al., 2016) as well as decreasing plant capacity to respond to abiotic stressors such as drought, warming, and frost (Fangmeier et al., 1994; Sardans and Peñuelas, 2012). Furthermore, changes in N:P ratio in foliar tissues can have several consequences in forest trophic chains (Peñuelas et al., 2013). For example, increases in foliar-litter N:P ratios have been associated with shifts in community composition and decreases in species richness in soil communities and understory vegetation in some European forests (Peñuelas et al., 2013). Unbalanced plant N:P ratios can reduce the resistance to biotic stressors such as the competition against invasive species (Sardans et al., 2016a).

### 4.1 Observational studies

The status and trends of tree nutrition are highly variable across Europe. At the European scale, two recent studies

report tendencies of decreasing foliar N concentrations for beech and oak, covering the periods 1992–2009 and 2000–2015, respectively (Jonard et al., 2015; Sanders et al., 2017b). To a lesser extent, decreases are also indicated for spruce, while stable or slight increasing foliar N concentrations are reported for pine (*Pinus sylvestris*). At the same time, however, the mass per needle/leaf significantly increased for spruce and beech, causing an overall increase in the N content per needle/leaf despite the decreasing concentrations (“dilution effect”, Jonard et al., 2015), frequently related to a rise in atmospheric CO<sub>2</sub> concentration (Peñuelas et al., 2020; Sardans et al., 2021a). At the local or regional level, studies based on data from 1990 onward report stable N concentrations or moderate changes in both directions (Jonard et al., 2012; Verstraeten et al., 2017; Wellbrock et al., 2016). Analysis restricted to, or including data from before 1990 frequently (Duquesnay et al., 2000; Hippeli and Branse, 1992; Mellert et al., 2004 for pine; Pritzel et al., 1997; Sauter, 1991) but not always (Braun et al., 2010; Mellert et al., 2004) report increasing foliar N concentrations or contents across Europe. Although not focused on temporal trends, other studies suggest a general effect of N deposition on foliar N concentrations based on analyses of large-scale spatial data (De Vries et al., 2003; Sardans et al., 2016b, 2021b).

Foliar P concentrations decreased continuously according to studies analyzing data from 1990 onward in the important forest species in central and northern Europe, such as pine, spruce, beech, and sessile oak (*Quercus petraea*), resulting in low or deficient foliar P status on 22%–74% of the plots depending on tree species (Ferretti et al., 2015; Jonard et al., 2012, 2015; Talkner et al., 2015). For N:P, increasing ratios have been observed in several studies at European scale based on data after 1990 (Du et al., 2021; Jonard et al., 2015; Sanders et al., 2017a; Talkner et al., 2015). Apart from N:P imbalances, also trends toward increasing N:K and N:S ratios have been observed in a Europe-wide study while the N:Mg ratio was decreasing (Jonard et al., 2015). N deposition can cause deficiencies in other nutrients than N and nutrient imbalances due to a range of effects, including stimulation of plant growth (dilution effect) and negative effects on tree nutrient acquisition by modifying mycorrhizal associations (De Witte et al., 2017; Jonard et al., 2015; Peñuelas et al., 2013; Sardans et al., 2016b). Du et al. (2021) observed an increase in the proportion of P limited plots from 25% to 33% when comparing tree nutrition data from 163 European forest sites between the periods 1995–97 and 2015–17. In the same study, the number of plots with N limitation was negligible. In addition to N deposition, there are also other drivers of global change underlying the foliar nutritional shifts of European forests. A more recent study on European forests showed that the increase in atmospheric CO<sub>2</sub> concentrations was well correlated with decreasing foliar N,



P, K, Mg and S concentrations (dilution effect) and increasing N:P ratio (Penuelas et al., 2020). These trends have a great variability mainly depending on latitude and climate, to the point that foliar N, S and Ca concentrations increased in northern Europe associated with increasing mean annual precipitation and temperature in the last decades (Penuelas et al., 2020). The European forests at mid (temperate forests) and low (Mediterranean forests) latitudes have experienced, instead, a decrease of the foliar concentration of most nutrients but not, or less, of N with the consequent imbalance in the N:other nutrients ratios. These decreasing tendencies in foliar concentrations of nutrients other than N and increasing N:other element ratios suggest that N availability is still high in many regions across Europe and do not imply a recovery from high N deposition yet.

## 4.2 Experimental studies

Besides observational studies, a number of experiments provide indication on the reaction of foliar element concentrations to decreased N supply. In one of the above-mentioned NITREX roofing experiments, a decrease in needle N concentrations and an improvement (reduction) of the N:Mg and N:K ratio is documented after 3 years (Boxman et al., 1998). At the other two sites, no significant reductions in foliar N concentrations were observed 6 years after the treatment started (Emmett et al., 1998). Högberg et al. (2006) report average foliar element concentrations for the time period seven to 12 years after the cessation of an N addition treatment. Foliar N concentration clearly decreased and other elements showed minor increases. Twenty years after termination of the N fertilization at the same site, foliar N concentrations were still slightly elevated compared to the control (Högberg et al., 2014). Similarly, Blaško et al. (2013) report a recovery (decrease) of foliar N concentrations based on measurements 17 and 19 years after the termination of an N fertilization experiment, while also still slightly exceeding the levels at the control plot. Results from grassland and moorland fertilization experiments report that foliar N concentrations had decreased when measured 7–15 years after cessation of the N addition (Clark et al., 2009; Edmondson et al., 2013; Stevens et al., 2012). These findings from experiments indicate that decreases in N deposition can be expected to be reflected in foliar N concentrations with a lag time of a several years.

## 4.3 Summary

Despite the large heterogeneity in trends in tree nutrition, studies based on large-scale long-term monitoring data report tendencies of decreasing foliar N concentrations for beech, oak and to a lesser extent for spruce. The degree to

which the decrease in N deposition contributes to these trends is not clear. On the one hand, decreasing tendencies of  $\text{NO}_3^-$  concentration in soil solution (see “Soil acidification and eutrophication”), findings from experimental studies as well as large-scale studies documenting the relation between spatial patterns of N deposition and foliar N concentrations suggest that the decrease in N deposition could have affected foliar N concentrations. On the other hand, the cutback in N deposition across Europe is typically far smaller compared to experimental treatments and might not yet have led to a widespread decrease in N availability for tree nutrition in a relevant magnitude (Braun et al., 2010; Mellert et al., 2017; Riek et al., 2016). The increase in foliar mass (dilution effect, Jonard et al., 2015), in the context of rising  $\text{CO}_2$  concentrations (Penuelas et al., 2020), likely explains a considerable proportion of the decrease in foliar N concentrations. Furthermore, decreasing tendencies in other elements and increasing N:other element ratios do not indicate recovery from high N availability. Further analyses are required to gain a better understanding where and to what extent changes in N deposition or other mechanisms control tree nutrition across Europe and which time lags are involved.

## 5. Tree vitality

Tree vitality can be defined as the plant’s capacity to grow and reproduce at a specific site (Körner, 2018), or as its capacity to restore the physiological efficiency after a disturbance (resilience, Lloret et al., 2011). Trees, as sessile long living organisms, are subjected to recurrent and fluctuating environmental stress factors, both biotic and abiotic, including pests, frost, drought, storms, soil fertility loss etc. Trees living in a sustainable forest ecosystem can overcome such disturbances by restoring their physiological efficiency, eventually through acclimatization processes (Bussotti and Pollastrini, 2021). Tree crown condition is often interpreted as an aggregated measure of tree vitality because it reflects the impacts of different environmental stressors (Eichhorn et al., 2016). Defoliation is the most important diagnostic parameter to assess crown condition and tree vitality in large scale forest monitoring programmes (Sanders et al., 2016). Defoliation, however, is an unspecific parameter, integrating the intrinsic genetic variability of trees, site effects, including soil fertility, climatic features, stand structure, and composition, and external factors, such as abiotic and biotic disturbances (Toigo et al., 2020) as well adaptive processes, e.g., decreased crown volume in beech (*Fagus sylvatica* L.) trees. Defoliation is not necessarily equivalent to physiological damage and can be considered indicative of the dynamic equilibrium of a tree in its own environment (Pollastrini et al., 2016). In a context of global change, the occurrence of external, anthropogenic additional disturbing factors can irreversibly

alter the ecological equilibrium of trees within communities and then ecosystems. Several fertilizer experiments and observational studies highlighted the relevance of N deposition as a factor potentially modifying the overall physiological status of trees and their responses to environmental pressures and disturbances over time.

## 5.1 Observational studies

Data from the pan-European forest monitoring network ICP Forests (Sanders et al., 2016) allow to explore the relationships between atmospheric N deposition and tree specific attributes, including crown condition. Analyzing this continental dataset, Seidling et al. (2015) found a high interannual dynamic of defoliation, resulting in difficulties to interpret correlation analyses, regressions, and other statistical approaches. Subtle effects, like those due to long-term N inputs, are masked by other stronger influences, such as climate and site factors. Ferretti et al. (2015) found that defoliation could be partly explained by N-related variables based on data from 71 monitoring sites across Europe: Higher N deposition in throughfall led to a higher percentage of defoliated trees for *Fagus sylvatica* and *Picea abies* (L.) Karst., while the opposite effect was found in *Pinus sylvestris* L. Vitale et al. (2014) found defoliation being related to N deposition for *Quercus ilex* L., *Pinus sylvestris* L. and *Q. Petraea* (Matt.) Liebl. stands, in addition to other factors like meteorology and age. Klap et al. (2000) only found a weak relationship for the impact of NO<sub>2</sub> on the defoliation of deciduous oaks (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.) and *Fagus sylvatica*. In a modeling exercise conducted by De Marco et al. (2014), N deposition was again identified as an important predictor for crown defoliation for several tree species. At national and regional level, Solberg and Tørseth (1997) found in Norway, Thimonier et al. (2010) in Switzerland, Hendriks et al. (2000) in the Netherlands, Staszewski et al. (2012) in Southern Poland, no or little effects of N deposition on crown conditions along N deposition gradients. Armolaitis and Stakenas (2001) report on the crown condition of a pine forest in relation to decrease of N emissions from a close-by fertilizer plant in Lithuania. Decreasing defoliation in damaged trees began 6–7 years after the decrease of air pollution.

## 5.2 Nitrogen-induced effects on vitality

Depending on the availability of N (and other nutrients) in forest ecosystems, increasing or decreasing N deposition can have different net effects on tree vitality. For example, improved N supply can enhance the photosynthetic activity and the synthesis of defense compounds, such as nonstructural carbohydrates (Huang et al., 2021). Therefore, in some experiments N counteracted damage and

promoted plant recovery after the impact of stress factors (Fusaro et al., 2017). On the other hand, excess N supply can cause a net decrease in tree vitality via complex, interlinked and potentially only episodically apparent mechanisms, including increased susceptibility to insect attacks, pathogens, frost and storm damages (Bobbink and Hettelingh, 2011; Jönsson et al., 2004; Li et al., 2016; Walter et al., 2021), changes in mycorrhiza (Arnolds, 1991; Braun et al., 2010; De Witte et al., 2017; Duquesnay et al., 2000; Jaenike, 1991; Kjølner et al., 2012; van der Linde et al., 2018), changes in the rooting system and aluminum toxicity to roots (Dziedek et al., 2017; Godbold and Kettner, 1991; Haynes, 1982; Jonard et al., 2012; Ostonen et al., 2007), depletion of base cations due to NO<sub>3</sub><sup>-</sup> leaching (Jonard et al., 2012; Priezel et al., 1997), increased vulnerability to tropospheric ozone (Marzuoli et al., 2018) and drought (Dziedek et al., 2016) as well as deficient P supply (Jonard et al., 2015; Mellert and Ewald, 2014; Neiryneck et al., 1998; Ochoa-Hueso et al., 2013; Peñuelas et al., 2013; Sardans et al., 2015; Sardans and Peñuelas, 2012; Thelin et al., 1998). Tree species, stand age, soil, and meteorological conditions as well as other local factors codetermine these symptoms. Under decreasing N deposition, tree response in terms of vitality will depend on the progressive reduction of N availability in the soil and the recovery of soil chemical, physical and microbial characteristics. These processes are very slow (Clark et al., 2009; From et al., 2015; Stevens, 2016).

## 5.3 Summary

Tree crown condition provides an aggregated measure of tree vitality. Studies evaluating spatial and temporal patterns of crown condition based on long-term monitoring data come to different conclusions regarding the relative importance and direction of the effect of N deposition. To our knowledge, no large-scale response to decreasing N deposition has been reported. N deposition can have both a positive (fertilizing) effect on tree vitality (crown condition) but also contribute to a range of adverse effects. We assume that the high complexity and spatio-temporal variability of these mechanisms is partly causing the difficulty to detect signals of decreasing N deposition in tree vitality. In addition, factors like site, stand age, drought, and frost can have strong effects on vitality independent of N deposition (e.g., Eickenscheidt et al., 2016; Klap et al., 2000).

## 6. Tree growth

Tree growth provides the primary economic benefit from most forest sites and is an important process in forest CO<sub>2</sub> budgets. Aber et al. (1998) hypothesized that net primary production of trees will show an increasing followed by a decreasing (unimodal) response with ongoing N saturation

(comp. Fig. 13.1). The underlying assumption is that low to moderate levels of N deposition will relieve trees from growth limitation due to originally widespread N shortage (Aber et al., 1995; De Vries et al., 2009; Kahle, 2008; Schulte-Uebbing and De Vries, 2017; Solberg et al., 2009; Sutton et al., 2008; Vitousek and Howarth, 1991). However, when N deposition exceeds a certain level, the stimulating effects diminish due to the antagonistic effects applying to overall tree vitality (see above), e.g., of soil acidification, nutrient imbalances and increased susceptibility to biotic and abiotic stress (Aber et al., 1998; De Vries et al., 2014; Dobbertin, 2005). For example, beneficial effects for tree growth by recovery from acidification have been documented in Europe and the US (Mathias and Thomas, 2018; Juknys et al., 2014).

### 6.1 Observational studies

There are various broad-scale and regional studies investigating the effect of N deposition on tree growth, while accounting for the impacts of other drivers, such as changes in temperature and precipitation (e.g., Braun et al., 2017; Kint et al., 2012; Kolář et al., 2015; Solberg et al., 2009). In these studies, changes in growth patterns have rarely been explicitly linked to declining trends in N deposition. In some cases, a simultaneous decrease in S and N deposition complicated the separation of effects (Juknys et al., 2014; Nellemann and Thomsen, 2001). However, the results of these studies provide indications for the threshold level of N deposition at which growth enhancement and growth reductions can be expected (Braun et al., 2017; Kint et al., 2012). For example, field monitoring data of forest growth at more than 300 plots in Europe suggest a nonlinear growth response to N deposition between 3 and 60 kg N ha<sup>-1</sup> year<sup>-1</sup> with a threshold near 35 kg N ha<sup>-1</sup> year<sup>-1</sup> (Solberg et al., 2009). Similarly, Etzold et al. (2020) report a unimodal response of forest increment to N deposition, with a change from positive to negative effects above around 30 kg N ha<sup>-1</sup> year<sup>-1</sup>. Their analyses is based on data from 442 forest plots from 23 European countries. Kint et al. (2012) documented a nonlinear growth response, in terms of basal area increment (BAI), to increasing N availability for 180 oak and beech plots in Flanders throughout the 20th century (the period 1901–2008). They found positive effects of N deposition on BAI up to 20–30 kg N ha<sup>-1</sup> year<sup>-1</sup> and declining growth above these levels. Etzold et al. (2014) found a nonlinear relation flattening off at sites with an N deposition above 20 kg N ha<sup>-1</sup> year<sup>-1</sup>, based on data from intensive monitoring plots in Switzerland. In experimental and observational studies in forests in Switzerland, Flückiger et al. (2011) found a growth-stimulating effect of N which turned into no effect or a decrease of growth with

increasing duration or magnitude of the N input. Anders et al. (2002), in Bobbink and Hettelingh (2011), reported growth-reducing effects of N deposition on Scots pine stands in the north-east of the German Northern Lowland in the vicinity of N emission sources with deposition rates exceeding 35 kg N ha<sup>-1</sup> a<sup>-1</sup>, while for other locations and tree species, accelerated growth was observed at open field deposition rates exceeding 10–15 kg N ha<sup>-1</sup> a<sup>-1</sup>. Flechard et al. (2020) analyzed the effect of N deposition on forest growth with a mechanistic model based on data from 22 CO<sub>2</sub> forest flux towers in Europe. They concluded that forest productivity decreases at N deposition rates above around 25 kg N ha<sup>-1</sup> a<sup>-1</sup>.

### 6.2 Experimental studies

Further information on the growth response of trees to different levels of N deposition originates from field experiments. For example, in one of the NITREX experiments, Boxman et al., 1998 report a significant increase in growth after 3 years of artificially decreasing N deposition rates by roofing. It should be noted, however, that in this experiment not only N but also S deposition decreased. Högberg et al. (2006) found that very high rates of N addition (90–180 kg N ha<sup>-1</sup> a<sup>-1</sup>) led to an increase in tree growth only until a cumulative amount of approximately 1 ton N ha<sup>-1</sup> while further N addition lowered the gain in wood volume. In a similar experimental setup, Blaško et al. (2013) observed that a strongly fertilized plot (90–180 kg N ha<sup>-1</sup> a<sup>-1</sup>) had a lower long-term average productivity than other fertilization levels (30–120 kg N ha<sup>-1</sup> a<sup>-1</sup>) but still more than the control plot. These results support the perspective that improved N supply has a positive effect on growth in case of N limitation and can act negatively in case of excess N (Flückiger et al., 2011).

Global meta-analyses also confirm thresholds in the growth response of trees to N deposition. For example, Tian et al. (2016) analyzed a dataset of 44 experimental studies from wetland, grassland, temperate, and boreal forest (most data are from temperate forest). They found that the effect of N input on aboveground net primary production switches from increase to decrease at approximately 50–60 kg N ha<sup>-1</sup> a<sup>-1</sup>. Schulte-Uebbing and de Vries (2017) found that the N-induced increase in carbon sequestration was significantly lower at higher ambient N deposition rates (above 15 kg N ha<sup>-1</sup> a<sup>-1</sup>), reviewing results from forest fertilization experiments in temperate, boreal, and tropical forests. Field data of maximum rates of photosynthesis against N deposition for 80 forested plots over the world indicated an increase in photosynthesis up to an N deposition near 10–15 kg N ha<sup>-1</sup> a<sup>-1</sup> followed by no further change up to 35 kg N ha<sup>-1</sup> a<sup>-1</sup> (Fleischer et al., 2013).

### 6.3 Summary

We did not find an indication for a large-scale response in tree growth to decreasing N deposition. However, results from observational and experimental studies corroborate the concept of a unimodal response of tree growth to N deposition. Estimates of thresholds above which N deposition negatively affects tree growth range from as low as 15–20 kg N ha<sup>-1</sup> a<sup>-1</sup> to very high levels only relevant under experimental conditions. This suggests that particularly polluted forest stands (mostly located in Central and Western Europe) might have benefitted from declining N deposition, as decreases have been strongest in the formerly most polluted regions. Few trends of decreasing N deposition have been observed in less polluted areas like Northern Scandinavia, suggesting that a growth decline due to decreased N deposition in these areas is less likely.

## 7. Conclusions and outlook

Results from observational studies across Europe for responses in soil, ground vegetation, and trees (nutrition, growth and vitality) to decreasing N deposition indicate considerable spatial variability in the trends published for these parameters. For soil solution NO<sub>3</sub><sup>-</sup> concentrations, indications for a reaction to decreased N deposition exist. The extent to which the observed reductions in foliar N concentrations are caused by decreasing N deposition is not clear, because increasing foliar mass (dilution effect in the context of rising CO<sub>2</sub> concentrations) also contributes to this trend. We found several studies reporting on the effects of N deposition on understory vegetation, tree growth or tree vitality, but none of them focused specifically on responses to declining N deposition. For tree growth, these studies suggest a positive effect at low to moderate levels of N deposition and no or adverse effects at high levels. In line with these findings from observational studies, experimental studies also report more pronounced responses of soil solution and foliar N concentrations to decreased N deposition compared to other parameters. Stevens (2016) reviewed experimental and observational studies in grasslands, heathlands, wetlands, and forests for information on the speed of recovery from high N deposition. Mainly in line with our findings, they report a relatively rapid response for mobile or plant-available forms of N in soil chemistry and for N contents in plant tissues across habitats (with the exception of forests showing a slower response in foliar element concentrations compared to other habitats). Similarly, Rowe et al. (2017) suggest N leaching rates and (moss) tissue N concentrations as midpoint-metrics, i.e., as indicators for effects-based monitoring of progress toward pollution reduction targets, due to their dynamic response to changing N deposition rates.

Linking results from observational and experimental studies is problematic due to the more controlled conditions and the typically faster and stronger cutback of N supply rates in experimental settings compared to real-world decreases in N deposition (Bebber, 2021). A multitude of confounding factors, including the joint decrease of N and S deposition (e.g., Armolaitis and Stakenas, 2001) complicate the interpretation of results from observational studies. Furthermore, many of the large-scale observational studies reviewed in this chapter are based on plots which are not distributed representatively across Europe. The larger monitoring efforts in Central and Western Europe likely led to an overrepresentation of plots where N deposition remained on a high level despite comparatively large decreases of N deposition.

Future decrease of N deposition to forests in Europe and associated ecosystem responses will most likely be limited (Fig. 13.3). Simpson et al. (2014) expect only minor reductions in the European ecosystem area with exceedances of the critical load for nutrient N (from 64% in 2005 to 50% in 2050). Under the assumption that soil solution NO<sub>3</sub><sup>-</sup> concentrations and potentially also foliar N concentrations track changes in N inputs with a delay of only a few years (see above), limited changes of these parameters in response to declining N deposition would be expected for the future. For tree vitality and vitality-related growth effects, time-lags in the recovery from excess N deposition might be expected due to slow reversal of N-induced soil acidification and changes in mycorrhizal association. For understory vegetation community composition it has to be questioned whether full recovery can be expected at all since forest biodiversity is facing a number of additional “extinction debts” such as habitat loss and fragmentation, climate impact, and nonnative species invasion (see e.g., Perring et al., 2017) likely causing further decline in biodiversity (Essl et al., 2015). Projections of understory plant species occurrence indicate that oligotrophic species will further decrease under current clean air legislation in Europe (Dirnböck et al., 2018). If at all, recovery processes will become apparent in regions with sufficient absolute magnitude of the cutback in N deposition and responses will likely be highly heterogeneous in space, controlled by site-specific conditions (Hedwall et al., 2021).

In view of our results, a simple reversal of the stages of the classical N saturation concept (Fig. 13.1) does not seem to reflect the observed and expected responses to decreasing N deposition appropriately. Instead, several forest ecosystem properties seem to react with varying degrees of delay to cutbacks in N deposition. Correspondingly, the overall forest ecosystem state develops on a different trajectory during the process of N desaturation compared to N saturation. This hysteresis behavior is in line



with findings from Gilliam et al. (2019), who reviewed results for soil acidification, plant biodiversity, soil microbial communities, forest carbon and N cycling, and surface water chemistry focusing on the US. A hysteresis behavior is also expected for the reaction of mycorrhizal fungi to changing N deposition (Suz et al., 2021). In view of the high variability of forest ecosystems, a set of “recovery types” could potentially serve to roughly classify the development of major strata of forest sites under decreasing N deposition. For analytic and predictive purposes, more detailed models will be required to adequately represent processes of N (de-)saturation. In particular, dynamic modeling approaches taking complex microbial soil N processes into account may provide insights into the developments of forest ecosystem N pools accumulated over the last decades (Akselsson et al., 2016; Bonten et al., 2016; Dirnböck et al., 2017; Fleck et al., 2017; Lucander et al., 2021; Rizzetto et al., 2016; Yu et al., 2016). Under the expected limited future decrease in N deposition, other controlling factors like climate change, rising atmospheric CO<sub>2</sub> concentrations, and forest management strategies will probably dominate the changes in N-enriched forests (Clark et al., 2019; González de Andrés, 2019).

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