Change, stability, and atmospheric pollutant effects in European forest vegetation

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Abstract

While the “acid rain” of the 1980s caused widespread damage to forests, the sulphur emissions responsible have been much reduced since. However nitrogen emissions remain at concerning levels, and there are also questions about how well ecosystems recover even after air quality improves. By using data from long-term monitoring projects, I investigated how understorey vegetation communities respond to disturbances including atmospheric pollutant effects, and how the concepts of ecological stability and resilience can help us understand this. First, the natural experiment of extreme natural disturbances at a monitoring site showed that surviving refuge areas act as “ecological memory” and contribute to resilience. Then I focused on lichens and bryophytes, which are known to be sensitive to air pollution. For lichens in Sweden, only limited recovery was found despite improved air quality, which may be due to a lack of nearby source populations to act as refuges analogous to those in the first study. Using data from sites across Europe I found adverse effects of nitrogen deposition in bryophyte communities. Finally, I tracked the stability of vegetation communities over time and found that the extreme disturbances in the first study were clearly visible but that the specific effects of atmospheric pollutants could not be seen in the vegetation community as a whole, despite the effects earlier found in the most sensitive parts of the community (lichens and bryophytes). These results highlight the importance of looking at sensitive sub-groups when looking for atmospheric pollutant effects, and the importance of long-term monitoring data in investigating these questions.

Keywords: Nitrogen, sulphur, community, plants, lichens, stability, resilience

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Abstract

Sedan 1980-talets "sura regn" orsakade omfattande skador på skogarna, har de ansvariga svavelutsläppen minskat avsevärt. Kväveutsläppen ligger dock kvar på höga nivåer, och det finns också frågor om hur väl ekosystemen återhämtar sig även efter att luftkvaliteten har förbättrats. Genom att använda data från långsiktiga övervakningsprojekt undersökte jag hur vegetationssamhällen reagerar på störningar inklusive luftföroreningar, och hur begreppen ekologisk stabilitet och motståndskraft kan hjälpa oss att förstå detta. För det första visade det naturliga experimentet av extrema naturliga störningar på en övervakningsplats att överlevande fristadsområden fungerar som "ekologiskt minne" och bidrar till motståndskraft. Sedan fokuserade jag på lavar och bryophyter, som är kända för att vara känsliga för luftföroreningar. Lavar i Sverige visade endast begränsad återhämtning trots förbättrad luftkvalitet, vilket kan bero på brist på närliggande källpopulationer för att fungera som tillflyktsorter som är analoga med dem i den första studien. Med hjälp av data från områden över Europa fann jag negativa effekter av kvävedeponering i bryophytesamhällen, inklusive förlust av mångfald. Slutligen spårade jag stabiliteten i vegetationssamhällen på ett antal områden över tid och fann att de extrema störningarna i den första studien var tydligt synliga men att de specifika effekterna av atmosfäriska föroreningar inte kunde ses i vegetationssamhället som helhet, trots de effekter som finns i de känsligaste delarna av samhället (lavar och bryophyta). Dessa resultat belyser vikten av att titta på känsliga undergrupper när man undersöker påverkan av luftföroreningar och vikten av långsiktiga övervakningsdata för att granska dessa frågor.

Keywords: Kväve, svavel, samhälle, växter, lavar, stabilitet, motståndskraft

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Dedication

To Z.

“So delicately interwoven are the relationships that when we disturb one thread of the community fabric we alter it all — perhaps almost imperceptibly, perhaps so drastically that destruction follows."

Essay on the Biological Sciences (1958)
— Rachel Carson

Contents

List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I. **Weldon, J**., Grandin, U. (2019). Major disturbances test resilience at a long-term boreal forest monitoring site. *Ecology and Evolution*, 9, pp. 4275– 4288

II. **Weldon, J**., Grandin, U. (2021). Weak recovery of epiphytic lichen communities in Sweden over 20 years of rapid air pollution decline. *The Lichenologist*, 53(2), pp. 203–213.

III. **Weldon, J**., Merder, J., Ferretti, M., Grandin, U.. (2021) Nitrogen deposition causes distinct eutrophication of European bryophytes (submitted)

IV. **Weldon, J**., Fried-Petersen, H. & Grandin, U. (2021). Community stability and airborne pollutants in forest understorey vegetation. (manuscript)

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The contribution of James Kurén Weldon (JW) to the papers included in this thesis was as follows:

I. JW contributed to the ideas and hypotheses and had the main responsibility for the analysis and summary of the results, and for the writing of the manuscript. JW was also corresponding author and had the main responsibility for incorporating reviewer comments.

II. JW contributed to the ideas and hypotheses, had shared responsibility for the analysis and interpretation, and the main responsibility for the writing of the manuscript. JW was also corresponding author and had the main responsibility for incorporating reviewer comments.

III. JW had the main responsibility of the ideas and hypothesis, and for the data analysis and interpretation as well as drafting the manuscript and incorporating comments and revisions from coauthors. JW is also the corresponding author.

IV. JW had the main responsibility of the ideas and hypothesis, and for the data analysis and interpretation as well as drafting the manuscript and incorporating comments and revisions from coauthors.

Additional publications

In addition to the papers included in the thesis, the author has contributed to the following peer-reviewed publications:

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Abbreviations and definitions

Ecological resilience	The ability of an ecosystem "to absorb repeated disturbances…and adapt to change without fundamentally switching to an alternative stable state" (Holling, 1973)
Ecological stability	"the ability of a system to return to an equilibrium state after disturbance" (Holling, 1973).

1. Introduction

While forests were once thought of as predominantly stable, as in the classical conceptions of a climax ecosystem created by succession processes (Clements, 1916), it has long been recognized that they are dynamic systems. Both natural and anthropogenic disturbances play a role in their dynamics and they can have multiple possible internal developmental pathways (Angelstam & Kuuluvainen, 2004; Taylor & Chen, 2011). As well as their influence on forest dynamics, natural disturbances also play an important role in sustaining biodiversity in forests as fires, storms and large-scale insect outbreaks create a mosaic of areas characterised by different habitats (Zackrisson, 1977), and shape the structure and function of forest ecosystems (Thom *et al.*, 2017a). While temperate and boreal forests have evolved in the context of natural disturbances occurring with varying intensities, intervals, and scales (Gutschick & BassiriRad, 2003) the pattern of disturbance is now much altered by anthropogenic factors, and natural disturbances are moderated by human activity in many areas. Fire is heavily supressed in much of Europe, even in relatively remote areas (Niklasson & Granström, 2000). Extensive efforts are also made to control outbreaks of damaging insects such as bark beetles (primarily *Ips typographus* in Europe), which are a major source of biotic damage to European forests (Schelhaas, Nabuurs and Schuck, 2003).

Aside from natural disturbances (which are often moderated by human influences), there are also purely anthropogenic disturbances which can strongly affect even unmanaged forest ecosystems. Climate change is altering moisture regimes, and interacts with many natural disturbances, such as increasing the frequency and intensity of fires and insect outbreaks (Seidl *et al.*, 2011). In the context of European forests however, perhaps the best-known anthropogenic disturbance has been the sulphur deposition commonly referred to as “acid rain” which generated widespread public concern during the 1980’s. This led to effective legislation to limit emissions and the establishment of monitoring schemes intended to improve understanding of how the long distance transport of atmospheric pollutants can influence the development of ecosystems and damage biodiversity (Grennfelt *et al.*, 2020). Considerable progress was made in reducing sulphur emissions (although these remain at levels that are potentially problematic in many areas (Engardt *et al.*, 2017)), but nitrogen emissions have proved harder to deal with effectively and remain a serious environmental concern (Erisman *et al.*, 2000; Bobbink *et al.*, 2010; Engardt *et al.*, 2017; Michel & Seidling, 2017; Dirnböck *et al.*, 2018). The anthropogenic input of reactive nitrogen on a global scale is enormous, a 2015 study for example estimated it to be approximately the same amount as all biological nitrogen fixation in unmanaged ecosystems (Fowler et al., 2015).

While disturbance factors such as these atmospheric pollutants have an impact on all aspects of forest vegetation from trees to lichens, the response is likely to be seen more quickly in organisms with a relatively short generation time. Both observational and experimental studies have looked at the impacts of atmospheric deposition of pollutants on forests, but high quality data is generally available for at most a few decades. Although changes in forest tree growth have been linked to N deposition (Etzold *et al.*, 2020), shifts in the relative abundances of tree species would be difficult to identify at this time scale. However, it is more feasible to measure shifts in the understorey plant community, which generally have much shorter generation times than canopy species. Apart from the question of response times, the vascular plants, bryophytes and lichens of the forest are important in their own right. While understorey composition is sometimes seen simply as a consequence of the dominant canopy species, understorey vegetation can strongly influence tree seedling establishment and nutrient availability for tree species, indicating that overall forest composition is the result of interactions between forest floor and canopy (Nilsson & Wardle, 2005; Landuyt *et al.*, 2019). In terms of forest functioning, the understorey vegetation plays a substantial role in overall forest productivity, nutrient cycling and evapotranspiration rates (Landuyt *et al.*, 2019). European forests are species poor compared to those in the tropics and much of North America but especially canopy species richness is low, particularly in the boreal region (Mauri *et al.*, 2017). Understorey plant communities therefore represent a large proportion of the biodiversity in European forest ecosystems (Gilliam, 2006), and are as a result also important for the ecosystem services these habitats provide (Hooper *et al.*, 2005).

1.1 Disturbances

Ecosystems are not static, but are dynamic systems shaped and governed by a range of disturbances. As the constituent species of a given ecosystem have evolved subject to the selection pressure applied by the disturbances acting on it over long periods, the community as a whole has some level of large-scale stability despite being subject to these disturbances. In a boreal forest subject to regular fires we would expect, for example, that pine species (which are somewhat resistant to fire) and their associated understorey plant communities would dominate over spruce (which is more vulnerable to fire) and its corresponding forest floor species.

Natural disturbances are of course not the only factors affecting forests, and in much of Europe silvicultural practices are an important consideration. Even in the small proportion of locations where there is no, or limited direct physical human intervention, anthropogenic stressors have a role to play. One widely discussed example is anthropogenic climate change, which is increasingly recognized as having serious effects on even remote and “pristine” forest habitats (McDowell *et al.*, 2020). Climate change is also known to interact with natural disturbances, in many cases aggravating their impacts (Seidl *et al.*, 2011; McDowell *et al.*, 2020). The long-distance transport of atmospheric pollutants is another such widespread disturbance factor, potentially having impacts even on sites that are formally protected from more direct human interference (de Wit *et al.*, 2015). Unlike natural disturbances, anthropogenic impacts have arisen over timescales too short for vegetation communities to adapt to them, resulting in disequilibrium between the environmental conditions and the vegetation community (Thom *et al.*, 2017b). While long-lived trees species are slow to respond (potentially implying an “extinction-debt” among species that rely on them (Kitzes & Harte, 2015)) species with short generation times typical of the forest floor will respond much more rapidly, and are therefore the focus of the papers included in this thesis.

Disturbances are often categorised as either diffuse, relatively slow drivers of change such as nitrogen or sulphur deposition, or short, sharp disturbances such as a storm or fire. These have been labelled respectively, press and pulse disturbances (Thom *et al.*, 2013). However a pulse event can have long-term effects best understood as a press disturbance, while a press disturbance can have an intensive phase best understood as a pulse (Donohue *et al.*, 2016), and viewing this difference as a gradient rather than a strict binary distinction may be more useful. In this conception, the chronic deposition of atmospheric pollutants is clearly closer to a press disturbance than a pulse, exerting a constant influence over many years, as opposed to the short severe impact of storm damage for example.

1.2 Atmospheric pollutants

Many temperate and especially boreal forest ecosystems are often nitrogen limited (Tamm, 1991; Vitousek & Howarth, 1991) and in many locations that is still the case, despite the general pattern of elevated inputs (Hyvönen *et al.*, 2008). However anthropogenic inputs of nitrogen have caused some areas of central Europe that were previously N limited to move to an N saturated state where growth is limited instead by phosphorus availability (Jonard *et al.*, 2015). In natural conditions of N limitation, there is a high degree of small-scale spatial heterogeneity in nitrogen availability which contributes to a higher diversity of plant species, while sustained atmospheric deposition entails a homogenous availability of nitrogen and a corresponding homogenisation of the vegetation community (Gilliam, 2006; Hülber *et al.*, 2008). Although vegetation community responses to increased N are variable, increases in graminoids and decreased dwarf shrub and cryptogram cover are often seen in European forests (Strengbom *et al.*, 2002; Bobbink *et al.*, 2010). Bryophytes as a group are especially vulnerable to changes in community composition (Bobbink *et al.*, 2003; Nordin *et al.*, 2005) and epiphytic lichens are also known to be particularly sensitive (Giordani *et al.*, 2014). Although nitrogen is a nutrient, it can also act as a stressor and reduce the resistance of some plant species to drought, frost damage, pathogens or herbivory (Nordin *et al.*, 1998; de Vries *et al.*, 2000, 2014).

Sulphur deposition effects are often described in terms of changes in soil chemistry, where acidification leads to the depletion of base cations (Bouwman *et al.*, 2002) but direct phytotoxic effects can also be seen in sensitive species. Many lichen species for example are especially sensitive, having an unprotected thallus surface and a non-specific uptake of mineral nutrients (Skye, 1979). In addition to this inherent sensitivity due to their basic biology, lichens also generally have a slow growth rate, and absorb more sulphur dioxide (SO_2) than vascular plants (Nash & Gries, 1991). As a result, they are quick to show adverse effects from sulphur deposition, resulting in their widespread use as biological indicators of air quality (Gilbert, 1986; Richardson, 1988).

One commonly used approach to assessing the impact of atmospheric pollutants is to define a critical load, 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, 1988). For example, the critical load for nitrogen in the context of temperate forest ground vegetation is currently considered to be 5-15 kg N per hectare per year, while the level for boreal coniferous forest is lower (2-3 kg N/ha/yr) due to the greater importance of sensitive lichens and bryophytes in this ecosystem. While these ranges are considered broadly applicable and are useful guidelines for policies aiming at reducing emissions to acceptable levels, it is also increasingly recognised that responses are variable and context dependant (Perring *et al.*, 2018; Hedwall *et al.*, 2021).

1.3 Ecological resilience and stability

While ecosystems are dynamic, there is logically a limit to the amount they can change while still being considered the same system (Scheffer *et al.*, 2001). The ability of an ecosystem “to absorb repeated disturbances…and adapt to change without fundamentally switching to an alternative stable state” (Holling, 1973) has often been used as a definition of ecological resilience. Similarly, stability can be defined as “the ability of a system to return to an equilibrium state after disturbance” (Holling, 1973). It should be noted that there is an extensive literature surrounding these terms, many alternative definitions and debate around whether stability is a subset of resilience or vice versa. While this is an important (and ongoing) debate, for present purposes I will use Holling's definitions. These concepts have often been visualised as a ball rolling around within a basin of attraction (the ecosystem's current stable state), where disturbances can serve to push the ball (ecosystem) over the lip of the basin and into a new basin of attraction (new stable state). Once the system tips over, in the same way that feedbacks and processes kept it within the first basin of attraction, other processes/feedbacks now serve to maintain the new equilibrium (Fig.1), and it may not be possible to return to the original state along the same path (the phenomenon of hysteresis (Scheffer *et al.*, 2001)). It follows that resilience in and of itself is not a beneficial quality, as the new equilibrium state may be undesirable but still resilient to remedial management (Angeler & Allen, 2016). While this works well as a conceptual model, such regime shifts have also been observed in nature such as the classic example of lake eutrophication leading to a rapid switch to a turbid state once a critical threshold is crossed (Scheffer *et al.*, 2001). However, there is also evidence that the existence of thresholds beyond which rapid change leading to a new equilibrium occurs may be less common than previously assumed (Hillebrand *et al.*, 2020). The resilience concept may then be most suitable for systems where there is some *a priori* reason to suspect that an alternative equilibrium is a possible outcome of disturbance (Paper I,IV) while stability is a more generally applicable concept (Papers II,III,IV).

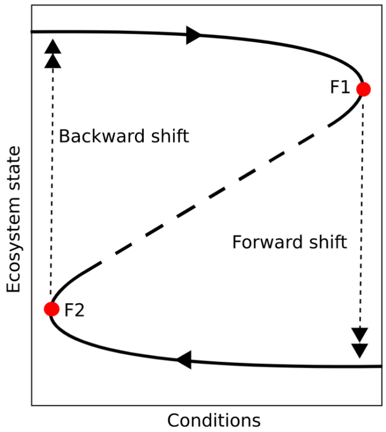

Figure 1: starting at the top left, a system with two possible states (upper and lower paths) may reach a critical point (F1) via incremental changes, at which stage it shifts to a new stable state (lower path). However, to return to the initial (upper) state, the other inflection point at F2 must be reached. This inability to reverse along the same path is known as hysteresis (adapted from Scheffer et al. (2001).

1.4 Why is "community" the appropriate response to consider?

In the papers presented in this thesis, I have generally used the vegetation community as the level of interest rather than individual species, that is to say the assemblage of species present at a given location and time of interest.

Different plant species each respond in their own way to disturbances and gradients in abiotic conditions, and this results in changes in the composition of vegetation communities, as the relative abundances of species which are tolerant or sensitive to that disturbance and the changed conditions it brings shift. This allows us to look at the community as a whole as a way of assessing the impact of a disturbance, or to focus on parts of the overall community that may be especially sensitive, such as epiphytic lichens (Paper II) or bryophytes (Paper III). While measuring the tolerance of a single species in a controlled setting to increased levels of a pollutant (for example) provides valuable information, plants in nature are always part of a community, and their response to disturbance is mediated by their place in a complex network of relationships and competition with other individuals and other species.

Furthermore, the community level view is essential in considering how disturbances relate to resilience and stability. There is a body of work suggesting that species richness and/or diversity is important in creating and maintaining stability (Lehman & Tilman, 2000; Wang & Loreau, 2016; Zhang *et al.*, 2018) and the presence of a wide range of species with differing responses to disturbances serves to stabilise ecosystem response to changed abiotic conditions (Hooper *et al.*, 2005).

2. Objectives

The papers included in this thesis aim to make use of the opportunities offered by large-scale long term monitoring to answer the following research questions:

- Using the natural experiment of multiple severe disturbances at a long-term monitoring site in Sweden we ask whether a combination of severe disturbances at a forest site suffice to shift the vegetation community into a new state, and if not, how is resilience demonstrated there? (PAPER I)

- The deposition of S and N has caused declines in sensitive species, with epiphytic lichens being especially affected. At four sites distributed across Sweden along an N and S deposition gradient, we investigate whether declines in deposition levels have led to a recovery of epiphytic lichen communities in terms of diversity and the presence/abundance of sensitive species? (PAPER II)

- N deposition effects on vascular understorey vegetation have been difficult to find in large scale observational data, and increased canopy shading has been suggested as a confounding factor. However, bryophytes are both generally more shade tolerant and more sensitive to N deposition. At a European scale, can a eutrophication signal and/or a negative impact of nitrogen deposition on forest bryophyte diversity be seen? (PAPER III)

- Using data from sites across Scandinavia and the Baltic region, we quantify and visualise forest floor vegetation community stability and investigate whether the deposition of airborne pollutants has an impact on the stability of vegetation communities. (PAPER IV)

3. Methods

3.1 Study sites and data

The studies presented in this thesis make use of data gathered by two long term monitoring programmes. These are the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests) and the International Cooperative Programme on Integrated Monitoring of Air Pollution Effects on Ecosystems (ICP IM), which fall under the Convention on Long-range Transboundary Air Pollution (Air Convention, formerly CLRTAP) of the United Nations Economic Commission for Europe (UNECE).

ICP Forests level II intensive monitoring involves 623 plots (as of 2018) in selected forest ecosystems across Europe, while ICP IM has 48 sites contributing data as of 2019. While all plots record the deposition of atmospheric pollutants (with N and S being of primary interest), coverage of vegetation data is less extensive, with some vegetation inventories being optional elements of the monitoring programmes. Bryophyte abundances are not recorded at many ICP Forests plots for example, while not all ICP IM sites record vegetation structure. In addition, some countries have participated for a period and then dropped out, while others have joined relatively recently. Consequently for a given set of variables of interest, only a subset of site/plot/year combinations will have suitable data. The common origin of the two monitoring schemes results in closely related and sometimes identical methodologies in terms of technical details such as the collection and chemical analysis of throughfall deposition. However inconsistencies can still arise and care must be taken when combining them.

Especially the harmonisation of species names can still be a challenge, as the data have been gathered over several decades during which the taxonomy of many plant species has changed, with those changes filtering through to the databases with varying delays. ICP IM data is used in Papers I, II and IV, while Paper III used a combination of ICP IM and ICP Forests data. Due to the differing focuses of the papers, geographic scope (and hence the number of sites/plots used) varies greatly. Paper I is based on one site in Sweden, Paper II on 4 Swedish sites, Paper III uses 164 sites across Europe and Paper IV is based on 10 sites in Scandinavia and the Baltic area.

3.2 Community responses

In order to assess vegetation community response, community composition at a given point in space and time must be quantified and summarised. I have used four main approaches, taxonomic diversity metrics (Papers I, II and III), functional diversity metrics (Papers I and III), community weighted mean preference indices (Papers I, II and III), and movements in ordination space (Papers I and IV).

3.2.1 Taxonomic diversity

Taxonomic diversity is measured as either Shannon diversity index (Paper I, II), calculated as

$$H = -\sum_{i=1}^{S} p_i \, log_b p_i$$

where p_i is the proportional cover of species i, and S is the number of species,

or Simpson diversity (Paper III), calculated as

$$D = 1 - \sum_{i=1}^{S} p_i^2$$

Both take into account species richness and relative abundance but rare species have a greater importance in Shannon diversity than in Simpson diversity, which can make it appropriate where rare species are of particular interest. However they are closely related (Hill, 1973) and in most cases the choice of index is not critical.

3.2.2 Functional diversity

Alongside these taxonomic based metrics, it can also be useful to focus on traits rather than species. If we are interested in the functioning of an ecosystem the identity of its component species may be less important than their functional role. If a species is removed from the system, it may be replaced by another species with similar traits, which implies that the system will function as before (Elmqvist *et al.*, 2003), although of course there may be other reasons such as conservation interest to be concerned about this replacement. Analysis of functional diversity can therefore be an interesting complement to focussing on taxonomic diversity. It also facilitates comparisons across large spatial scales encompassing different species pools, as communities which have similar distributions of traits will appear similar in analyses even when those traits are represented by different species.

As with measures of taxonomic diversity discussed above, there is a wide range of proposed metrics for quantifying functional diversity (Petchey *et al.*, 2009). The use of these metrics is further complicated by the fact that results are equally affected by the choice of traits used to calculate them. Depending on the species of interest, there may be data available on a wide range of traits such as reproductive method, seed size, leaf area and many more. Given this wide choice of both metrics and variables there is no single correct approach. Where I have analysed functional diversity changes in communities of interest (Paper I, III) I have used “umbrella” traits - broad traits (growth form, life form, and life strategy) that would be expected to capture much of the variation in a larger number of more specific traits while being more universally applicable. Functional classifications used were growth form (prone, upright etc.), Raunkiær life form (Raunkiaer, 1934) and classification in Grime's CSR model (Grime, 1977). The first two combine to give a relatively simple summary of a species’ morphological characteristics, while the latter is based on plant strategies for dealing with stress or disturbance.

These selected traits are then used to calculate indices of functional diversity. Functional evenness (FEve), functional richness (FRic) (Villéger,Mason & Mouillot, 2008), functional dispersion (FDis) (Laliberté & Legendre, 2010), and Rao's quadratic entropy (RaoQ) (Botta-Dukát, 2005) are used. These indices are all different approaches to quantifying the relationships between the species present in a community in multidimensional functional trait space, that is, measuring the spread of points (i.e. species) in an n-dimensional trait space. FDis and RaoQ estimate the dispersion of species in that space, weighted by relative abundances, FRic is the multidimensional volume occupied by the community and FEve is the regularity of abundance distribution in this volume. These metrics are explored in Paper I. In Paper III, I concentrate on Rao's quadratic entropy as a measure of functional diversity (which is closely related to FDis).

3.2.3 Community weighted mean preference/optima metrics

Another approach is to quantifying community response is to use the environmental preferences for each species present to create a community weighted mean. Classifications are available for species on a scale according to their ecological optimum along a gradient of e.g. N availability (Ellenberg *et al.*, 1992; Wirth, 2010), or tolerance to sulphur (Hultengren *et al.*, 1991). As levels of N or S increase the most sensitive species become less abundant or disappear altogether, while tolerant species increase in abundance or enter the community, processes which are reflected in changes in the community weighted mean preference/tolerance for N or S changing (Diekmann, 2003). Changes in community mean Ellenberg/Wirth N value are analysed in Papers I, II and III, and change in Hultengren S sensitivity index is also used in Paper II.

3.2.4 Ordination scores

The main aim of ordination analyses is dimensionality reduction, which is of obvious value when the focus of interest is all the species present in a community. Rather than considering each species individually we can summarise and/or visualise the community as a whole at a given location and easily relate that location to others and/or to gradients in abiotic variables. In Paper III we used Principal Components Analysis (PCA) as an exploratory method to visualise the relationships between our explanatory variables. In Paper IV we used PCA in a different way, tracking the distance moved by individual plots through the ordination space over time as a measure of stability, relating the shapes created to conceptual models of resilience, and using the distance from the baseline of the first observation as a response in a model with N and S deposition as predictors. PCA is commonly applied to data with a linear response (e.g., abiotic data) while unimodal responses are more common in biological data. However, Legendre & Gallagher (Legendre & Gallagher, 2001) demonstrate that PCA on Hellinger transformed data is suitable for finding gradients in biological data. While the relative merits of ordination methods have been much discussed in the context of placing communities at appropriate locations in an ordination space with axes reflecting resource gradients, in Paper IV we are interested solely in the position of a plot relative to itself earlier in a timeseries as a way of tracking stability. In Paper I, non-metric multidimensional scaling (NMDS) was used in order to explore the divergent developments of the refuge and non-refuge plots after the disturbances at the study site. Both approaches are widely applicable but in contrast to PCA, which uses raw data (or transformed raw data) to calculate distances, NMDS takes a distance matrix (here Bray-Curtis distance (Faith *et al.*, 1987)) and applies an iterative, rank-based algorithm to produce an ordination.

3.3 Statistical analyses

All analyses were performed in the R environment, versions 3.4.4 – 4.0.

In Paper I, we used a range of methods to investigate whether and how the vegetation community had changed following the extensive disturbances at the study site. We tested for differences in community composition between years and between areas identified as potential refugia and other plots using permutational multivariate analysis of variance (PERMANOVA). Differences in taxonomic and functional diversity and in community weighted mean Ellenberg N value between years and between refugia/non-refugia were investigated using ANOVA. To investigate which species best characterised communities and whether this changed with time or with refuge status, we used indicator species analysis, a method which assigns an indicator value to all species present based on their relative average abundance in clusters and ranks them accordingly.

Temporal trends in Shannon diversity index and in the community weighted mean N and S preferences were assessed in Paper II using linear mixed models (Pinheiro et al.2019) to account for the nested nature of observations and a first order autocorrelation structure to compensate for repeated observations by assigning time as a continuous covariate.

When focussing on the association between atmospheric pollutant levels and community response we assessed the relationships between response and our hypothesised explanatory variables using generalised additive models (GAMs) (Paper IV) and quantile generalised additive models (qGAMs) (Paper III) in two of the papers. The main advantage of these approaches is that the response is not limited to a linear relationship (although this is allowed for), and can follow e.g., unimodal or even bimodal patterns in the data. They couple this flexibility with the same possibilities offered by generalised linear models (GLM) and generalised linear mixed models (GLMMs) such as categorical predictors, interactions, and autocorrelation and/or hierarchical structures (Wood, 2006). qGAMs are a recent development and offer the further advantage of not demanding a pre-defined error distribution (Fasiolo *et al.*, 2020).

4. Results and Discussion

4.1 Diversity and disturbance

The effect of disturbance on diversity is conditional on the nature of the disturbance and the community of interest. In Paper I the combined effect of storm damage and bark beetle attack created a more heterogeneous environment, with newly opened areas alongside surviving pockets of forest. Here the site as a whole saw increased functional and taxonomic diversity as ruderal herb and shrub species colonised areas with increased light and nutrient availability, alongside persisting forest specialists. While the Aneboda site that is the focus of this paper has also experienced N and S deposition, the other disturbances at the site make it difficult to separate out any signal that could be found of their effects.

In Paper II the area with highest N and S deposition levels showed declining taxonomic diversity of epiphytic lichens, despite falling deposition levels, while the site which has never experienced high deposition showed no change in taxonomic diversity over time (Table 1). However, the declines in diversity are best characterised as occurring early in the monitoring period (when deposition levels were highest) followed by a failure to recover as deposition levels declined. We suggest that the reason for this could be that the atmospheric deposition of pollutants is a disturbance on a wide geographic scale and affects the whole regional species pool. Given that many epiphytic lichen species have limited capabilities for dispersal and/or establishment (Dettki *et al.*, 2000; Sillett *et al.*, 2000; Öckinger *et al.*, 2005), recolonisation may be hindered by a lack of nearby source populations and suitable habitats for dispersal, despite the improvements in air quality. This also has potential implications for the common practice of using sensitive species as bioindicators of air quality. While they work well as bioindicators of worsening air quality (Skye, 1979), they may be less reliable as indicators of improving air quality. Other studies have found both recovery broadly in line with air quality (Pescott *et al.*, 2015) and dispersal and/or establishment limitation (Hawksworth & McManus, 1989; Öckinger *et al.*, 2005) hindering recovery despite cleaner air.

A negative association between taxonomic diversity and N deposition levels was found also in Paper III for bryophyte communities at sites across central and northern Europe. We found the highest diversity at plot/year combinations with the lowest deposition levels of both ammonium and nitrate. Negative effects were moderate, at most a 15% decline in diversity, and nitrate showed a somewhat stronger effect than ammonium. Their combined effect across a range of moderate deposition levels is less than cumulative, i.e., the two N species have a stronger impact acting in relative isolation. Strongly species specific responses to nitrogen (Gordon *et al.*, 2002; Salemaa *et al.*, 2008) and to specifically ammonium or nitrate (Paulissen *et al.*, 2004; Hawkins *et al.*, 2018) have been found, suggesting that the impact of N deposition on diversity will depend on community composition, with some assemblages more affected by ammonium or by nitrate. Some species are unable to respond to N addition by increasing growth and instead accumulate amino-acids in harmful concentrations (Nordin *et al.*, 1998, 2005). An overall negative effect of N deposition on diversity is in agreement with other studies that have shown a decline in growth due to N inputs in sensitive species adapted to N poor conditions (Strengbom *et al.*, 2001; Gordon *et al.*, 2002; Nordin *et al.*, 2005) and a long-term negative effect even after N inputs have ceased (Nordin *et al.*, 2005). It may also be the case that N deposition adversely affects bryophyte diversity by favouring vascular competitors such as grasses better able to make use of increased N availability (Strengbom *et al.*, 2002; van der Wal *et al.*, 2005).

The relationship with functional diversity was less straightforward, with a general pattern similar to that found for taxonomic diversity (i.e. a declining diversity with increasing N deposition), but some plots showed high diversity despite high levels of deposition. This suggests that at least some of the species lost or declining (as indicated by reduced taxonomic diversity) are functionally redundant. Given that the traits used to calculate functional diversity were broad morphological traits (growth form, life form and life strategy) it is not surprising that a high degree of redundancy can occur at some locations.

While taxonomic diversity indices such as Shannon and Simpson are informative, it is also possible to decompose changes in beta diversity into components of turnover and nestedness (Baselga, 2010). This is useful as changes in beta diversity are driven by both species turnover (where some species are replaced by others) and community homogenisation (where the species poor plots are a strict subset of the species rich plots). This was done in Paper II and demonstrated that there has been a decrease in turnover and an increase in nestedness at the site with highest N and S deposition levels, indicating a homogenisation of the lichen community (Table 1). The sites with lowest deposition, however, were stable for both turnover and nestedness. In the context of large reductions in deposition levels at the previously polluted areas it is concerning that homogenisation has increased in the most recent survey. Finally, the disturbed site (Aneboda) showed, as expected, a large increase in species turnover as ruderal species colonised the area post-disturbance.

Table 1. Summary of mixed model results for epiphytic lichen sensitivity to N and S deposition at monitoring sites in Sweden. Sites arranged by decreasing deposition levels. Minus sign indicates a significant decrease, while a plus sign indicates a significant increase.'n.s.'indicates a non-significant change. (Paper II)

	Gårdsjön	**Aneboda**	**Kindla**	**Gammtratten**
S sensitivity	+*	n.s.	-**	-*
S-sensitive species	n.s.	-**	n.s.	-*
N preference	-*	n.s.	+*	n.s.
N-sensitive species	n.s.	-**	n.s.	n.s.
Shannon diversity	-*	-**	n.s.	n.s.

∗) $P < 0.05$, ∗∗) $P < 0.01$

4.2 Community weighted mean preferences/optima

At the disturbed Aneboda site (Paper I) there was an increase in mean Ellenberg N value across all plots at the study site taken as a whole. However, when comparing refuge areas to disturbed areas, communities in the latter had a higher mean N preference, as nitrophilous ruderal species colonised. Large amounts of N are made available for field layer vegetation as trees die, reducing demand from tree species and increasing litter (Karlsson *et al.*, 2018). While at N saturated sites this can result in greatly increased N leaching, here the vegetation has taken up the extra N and leaching has been very limited (Mikkelson *et al.*, 2013; Löfgren *et al.*, 2014). In this case the possible impact of anthropogenic N deposition is masked by this large post-disturbance mobilisation of N at the site.

In Paper II, we found that the mean N preference of the epiphytic lichen community had decreased at the most polluted site, in line with reduced deposition, but had increased at a site with consistently lower deposition levels (Table 1). The area that had seen very low deposition levels throughout the monitoring period showed no change. We also analysed community mean sensitivity to SO_2 in Paper II (Hultengren sensitivity index) and found that although the most polluted site showed increased mean S sensitivity (i.e., an increase in sensitive species, a decrease in tolerant species, or both) two sites with lower past and present deposition levels had declined in mean sensitivity over the study period, including the site in the north that is considered "pristine". While the most polluted site showed an improvement, this was driven by a loss of tolerant species rather than an increase in sensitive species, and the decline in the least polluted site is concerning. The discussion in the diversity section above regarding the limited ability of sensitive species to recolonise despite apparently suitable environmental conditions is also relevant here.

In Paper III we found evidence of a eutrophication effect, an increase in community mean N preference in bryophytes with increasing levels of N deposition. By modelling the interaction between the two forms of N measured, it appeared that nitrate had more impact in shifting community mean preference than ammonium, but that both forms of N have a stronger effect when acting in relative isolation rather than a simple cumulative impact. The high level of species specific variation in uptake of N (and in ammonium relative to nitrate (Hawkins *et al.*, 2018)) may explain this, with the bryophyte community at a given location potentially being more sensitive to ammonium or nitrate deposition depending on its composition (see discussion of Paper III, compositional changes, in section 4.1, which is also applicable here).The effect size seen was modest, with at most a 25% increase in community mean N Ellenberg value despite our focus on bryophytes which as a group are more sensitive to atmospheric pollutants than vascular plants (Nordin *et al.*, 2005; Bobbink *et al.*, 2010). One reason suggested for limited or no eutrophication signals found in other studies (largely focussed on vascular plants) has been that N deposition results in increased canopy growth, limited light and therefore limited response in the understorey vegetation (Jonard *et al.*, 2015; Binkley & Högberg, 2016; Gilliam, 2019). While bryophytes were chosen for this study partly as they were more likely to show a response even under conditions of light limitation, and canopy cover is included as a variable in the models, we cannot exclude a dampening effect on the eutrophication signal found (which may also come from the shading caused by the shrub or herb layer). Another factor that is likely relevant is that N deposition was elevated even at the start of the monitoring period, with a corresponding baseline shift for later observations. Relative to sometimes large existing N pools the relatively small size of annual N deposition can have limited impacts on vegetation composition (Diwold *et al.*, 2010). Clearer eutrophication effects have been found in vascular species by focussing on the exceedance of critical loads for N rather than current deposition levels (Dirnböck *et al.*, 2014), which may also be applicable to bryophyte communities. Another recent study based on herb-layer forest vegetation found that N deposition drives the extinction of specialised N-efficient species with small ranges and increases in nitrophilous plants with broad geographic distributions (Staude *et al.*, 2020), and it is possible that the same process is affecting bryophyte communities.

4.3 Stability, resilience, and disturbance

The disturbed spruce (*Picea abies*) dominated forest site, Aneboda, which is the focus of Paper I can plausibly be considered as having the potential to flip to an alternative stable state. At this site beech (*Fagus sylvatica*) was common in the shrub layer long before the disturbances and we hypothesised that the increased light availability and release from competition from spruce might facilitate a rapid establishment of beech as the dominant tree species, supressing the re-establishment of spruce. This is a process which has been observed in the region (Bolte *et al.*, 2014). While the ordination (NMDS) analysis of community composition shows only limited changes over the site taken as a whole, this masks an increasing divergence of the disturbed areas and the refugia where the disturbance impact has been very limited. In the disturbed areas ruderal species able to rapidly colonise and make use of the post-disturbance regime of increased light and nutrient availability have shifted the community composition (Fig. 2). However, the previously dominant tree species, spruce, is regenerating strongly and it appears unlikely that beech will be able to supplant it as the dominant canopy species. A single larger plot at the site that is part of a parallel sub-programme of vegetation monitoring features in Paper IV, where a strong directional movement over time in the ordination space is demonstrated, indicating low stability. This plot is located in a disturbed area and this movement/low stability reflects the changes outlined above in the non-refuge plots. If the conclusions of Paper I prove correct over the long-term, we would expect that as the spruce canopy re-establishes, conditions on the forest floor will facilitate a return to the pre-disturbance community and this plot will eventually return to roughly the same area in ordination space as it occupied pre-disturbance (Paper IV), just as the divergence of refugia and non-refuge plots should reverse (Paper I).

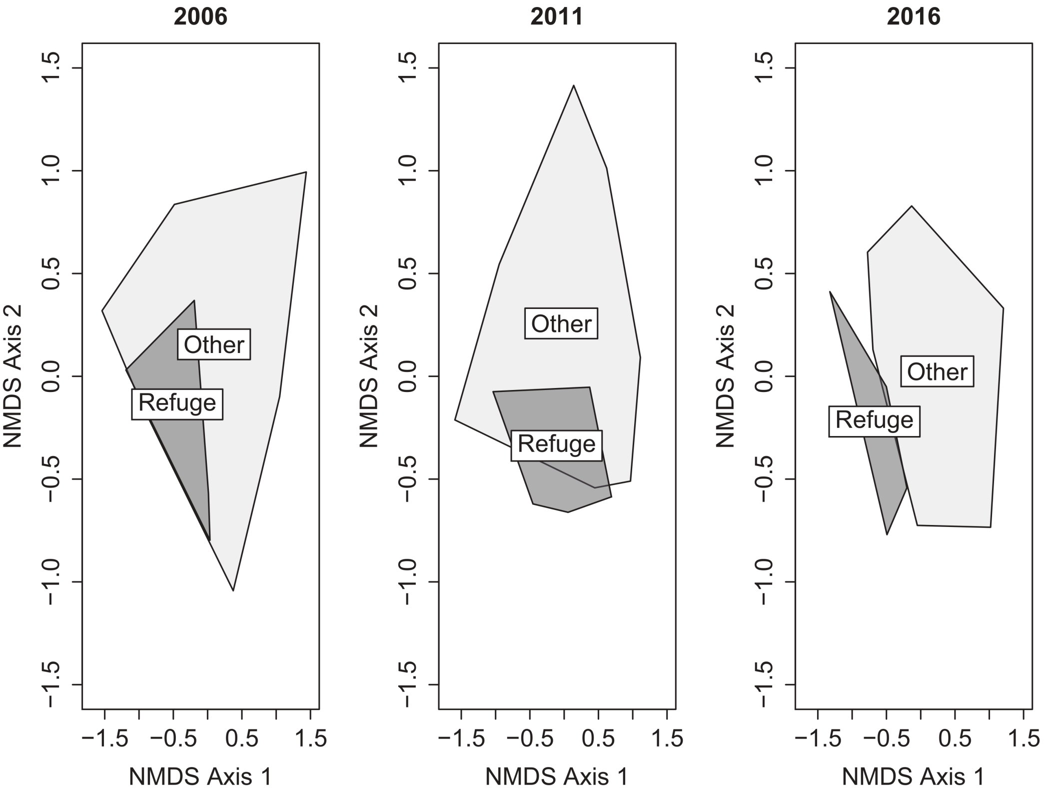

Figure 2: nMDS of ground layer plots with convex hulls indicating refuges and non-refuges, showing an increasing separation of refuges and non-refuges over time, convex hulls drawn from points representing plots, Bray–Curtis dissimilarity (stress 0.11, 0.12, 0.11). From Paper I.

While the conceptual model of resilience theory posits alternative basins of attraction in the abstract, in a given real-world situation there are of course constraints and context dependency. The local and regional species pools, environmental conditions and the nature of the disturbance are all important here. In a spruce forest for example, we could consider the possibility of a disturbance catalysed shift to beech dominance as in Paper I. However, this possibility is created by windthrow and bark beetle attack, while an equivalently severe disturbance caused by fire would create other possibilities. The alternative basin of attraction then would be a pine (Pinus sylvestris) dominated state, given that pine is also abundant at the site, resistant to fire and thrives in open areas (Angelstam & Kuuluvainen, 2004). A shift to this new stable state would require a long-term change in disturbance (fire) regime however, if the pioneer pine forest is not to later revert to spruce dominance.

Papers II and III focus on eutrophication and acidification effects, which can also be related to stability. A vegetation community that is shifting strongly over time to a different composition whether by becoming less diverse, more homogenous, losing N or S sensitive species, and/or gaining N or S tolerant species is not a stable community. At the same time, it is important to be aware that short term changes may reflect the random movements of the community "ball" within its basin of attraction. Long term strongly directional changes however may indicate not only low stability but in a system with alternative stable states, insufficient resilience to prevent a move to another basin of attraction.

This possibility is the focus of Paper IV, where I tracked the movement of plots in ordination space across time to visualise stability and potential shifts in state. The strong effects of the storm and subsequent bark beetle attack at Aneboda are clearly visible as the plot begins a rapid post-disturbance directional movement away from its starting position (Fig. 3). Most other sites appear rather stable, with apparently random movements within a small area, but there are exceptions (albeit nothing as obvious as Aneboda). I tested the hypothesis that the deposition of N or S decreases community stability by using a plot's movement in ordination space relative to the previous observation as the response in a GAM model with either N or S deposition as explanatory variable. There was, however, no significant association between either N or S deposition and decreased (or indeed increased) stability. This suggests that at least in the moderate deposition sites included, the impact of atmospheric pollutants is not strong enough to move the position of communities in the ordination space, while more extreme perturbations such as windthrow and bark beetle attack have a clearly visible effect.

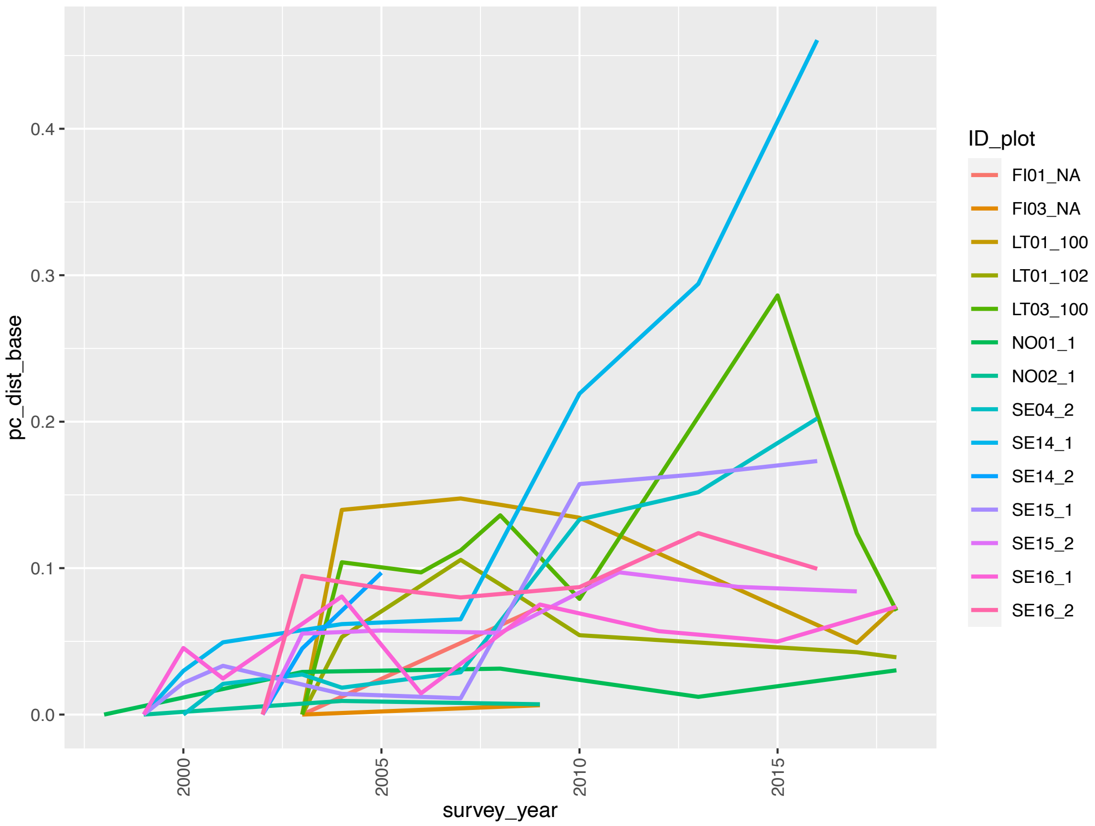

Figure 3: Distance moved in ordination space over time, from the baseline of the first observation. The disturbed site at Aneboda (SE14_1, light blue) stands out as having low stability, indicated by constantly increasing distance moved from baseline. From Paper IV.

4.4 Ecological memory

Paper I demonstrates the divergence of the refuge and non-refuge plots at a single disturbed site, with the refugia acting as a form of ecological memory (Allen *et al.*, 2016; Jõgiste *et al.*, 2017), from where the forest species (and particularly the pre-disturbance dominant tree species *Picea abies*) can begin recolonising disturbed areas. (Fig. 2). In Paper II however, we see evidence of a failure of an analogous process at a regional scale. Here, despite the decline in airborne pollutant levels creating an apparently suitable environment for sensitive species of epiphytic lichens, the recovery of lichen communities has been limited. Many lichen species have limited dispersal and/or establishment capabilities and are slow to spread across a landscape. Given that airborne pollution has negative effects on populations at a regional scale we suggest that the lack of nearby population sources of sensitive species (which we could consider as refugia) may be delaying recovery at the affected sites. Dispersal rates and the size of the disturbed area are important considerations in how recovery after perturbation occurs (van de Leemput *et al.*, 2018).

4.5 Monitoring schemes and disturbances

The details of monitoring schemes can influence the results found. One of the Swedish monitoring sites, Aneboda, which is the focus of Paper I and is also featured in Paper IV, has data available from two vegetation subprogrammes that are part of the ICP IM programme. One of these involves circular plots distributed in a grid across the entire site (and is optional in the monitoring scheme), while the other involves two smaller, intensive plots of 40m x 40m. While the former is more extensive and gives an overview of the whole site, the intensive plots are more likely to capture all species present and changes in their relative abundances. However by being inherently limited in spatial coverage, the intensive plots can fail to capture the impacts of spatially heterogenous disturbances across the site as a whole. The disturbances at Aneboda created a mosaic of relatively undisturbed patches and open areas where most or all trees were lost, and the one intensive plot that survived the disturbance is located in a relatively open area. While ordination analysis of the site as a whole (extensive, circular plots) shows no large shifts in community composition, this can be decomposed into an increasing divergence between the refuge and damaged areas (Paper I). Not being located in a refuge area, ordinations of the intensive plot show strong directional change over time (Paper IV) but gives only a partial indication of the development of the overall site post-disturbance. While having both these complementary vegetation sub-programmes available makes this clear, it is important to realise the possibility for mismatches between the details of a monitoring scheme and the effect that is being investigated. It should be noted that the aim of the ICP IM vegetation monitoring is principally to assess the effects of atmospheric pollutants, which are not spatially heterogenous at the level of a monitoring site but monitoring data has been and will be adopted for uses beyond those for which the programme was originally designed.

5. Conclusion

As was demonstrated during the peak period of "acid rain" during the 1980's, the long-distance transport of atmospheric pollutants clearly has the capability to act as an agent of large scale and extreme disturbance (Grennfelt *et al.*, 2020). However, under current levels of deposition in Europe their effects are more subtle, but absolutely not negligible. The loss of the most sensitive species will not result in anything that could be described in the language of resilience theory as a regime shift of the vegetation community but is nevertheless a loss of diversity and a cause for concern. Eutrophication effects such as an increased proportion of nitrophilous species can result in homogenisation of communities and a decline in diversity. If taxonomic and functional diversity is a source of resilience in vegetation communities, its loss will leave them more vulnerable to disturbance, although as we have seen the relationship between diversity and resilience is also scale dependant. Where disturbance results in a mosaic landscape in terms of conditions and resource availability, more niches are created and higher diversity sustained, while a smaller homogenous area may show only a decline in diversity.

The forest canopy is vital in regulating many of the resources most important in determining the composition of forest floor/understorey vegetation communities (although this is also a two-way interaction). Light is the most obvious of these, but also temperature, moisture, soil chemistry, nutrient inputs and substrates for epiphytic species all play important roles and are mediated by canopy species. Drastic changes in the canopy caused by disturbances such as storm damage or insect attack have effects on the non-canopy vegetation that swamp any effect from atmospheric pollutants, and when tracking forest floor community stability over time, only these extreme changes could be seen as a clear direction shift. However, I have also demonstrated that the deposition of atmospheric pollutants results in reductions in bryophyte and epiphytic lichen diversity, and in shifts in community composition as pollution tolerant species increase at the expense of those that are sensitive. Furthermore, it is not given that simply reducing emissions of pollutants is sufficient to restore damaged communities, which can show adverse effects for many years (and potentially many decades) after reductions occur. The impacts of atmospheric pollutants under current deposition levels are not as obvious as the dead forests and lakes of the 1980's which prompted the establishment of monitoring schemes, but it is precisely the existence of consistent high-quality data covering long periods that enables the more subtle adverse effects to be investigated. Although established principally to monitor sulphur deposition, as nitrogen became a more pressing concern the monitoring sites again proved important and will only become more valuable in future, as long as consistency can be maintained.

5.1 Future Directions

The effects of atmospheric pollutants on understorey vegetation are complex. As attention was focussed on the problem, the initial expectations that many researchers had of a clear large scale eutrophication effect were not confirmed, and it became increasingly clear that a range of interactions and confounding factors were involved. Effects have subsequently been found in sensitive sub-groups such as low-N adapted vascular plants, bryophytes and lichens (including in the studies presented here), but there is a great deal of scope for further studies which tease apart the interaction of deposition with factors such as climate change, land use history, herbivory and more. There is also potential for further investigation of the relative impacts of ammonium and nitrate on community level response. These two N species have most often been treated as a combined total, but species-specific variation in responses are well known (e.g. Hawkins *et al.*, 2018). At the level of functional groups, a recent meta-analysis of N effects (Yan *et al.*, 2019) found that ammonium generally has a stronger positive effect on biomass increase than nitrate but that for grasses nitrate had a stronger effect, but the authors did not include lichens and bryophytes due to lack of data, indicating an area for future studies.

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Popular science summary

You have probably heard of “acid rain”, which was a huge issue back in the 1970s and 80s (and still is in some parts of the world). Sulphur emissions from industry, traffic, and other sources travelled long distances and fell back to earth as acidic rain, damaging or kiling lakes and forests. Unlike some of the environmental issues we face today, there was prompt and effective international co-operation to solve the problem and sulphur emissions were rapidly reduced. While this was a success story, scientists noticed that sulphur wasn’t the only problem. Nitrogen was also being emitted by traffic and agriculture (among other sources) and could also travel long distances before coming back to earth. And while sulphur levels had gone down a lot, nitrogen levels had not. Nitrogen is a fertiliser, which sounds like a good thing but can cause a lot of problems. The normal state of most forests is that nitrogen is a scarce resource, and lots of plants have evolved to cope with low levels of it. Suddenly having lots of it available can mean that these plants find it hard to survive, either because too much nitrogen is directly harmful or because other plants that prefer high levels of nitrogen out-compete them. These kind of changes could have serious consequences, for the diversity of plants and the animal species that rely on them, and for the useful functions and services that forests provide.

In European forests there are relatively few different tree species, and most of the plant biodiversity is in the grasses, herbs, bushes, mosses and lichens. Also, because trees generally live for a long time, it could take many decades for the effects of pollutants to be seen. In contrast, we can see changes in the forest floor vegetation much more quickly, so that’s where we looked in these studies. While it can be important to look at what is happening to a particular plant species, in nature they don’t exist in isolation. They are always interacting with other species in complex ways, so we talk about the plant community, and this community is where we looked for evidence of changes.

As well as investigating whether pollutants were causing changes in these communities, we were also interested in how much disturbance they can cope with. Here we talk about two closely related concepts, ecological stability (how well an ecosystem can recover after disturbance) and ecological resilience (how much disturbance the system can absorb without becoming a fundamentally different ecosystem).

In Paper I we looked at a Swedish forest that was hit by both a serious storm and an outbreak of tree-killing bark beetles. It seemed possible that it could switch from being mostly spruce to becoming a beech forest. We found that although the vegetation has changed a lot in the disturbed areas, there were some areas that had escaped most of the damage. These were helping spruce and other species recolonise, acting like "ecological memory". This suggests that this forest was resilient to even extreme disturbances (at least over the long term). In Paper II and III we focussed on two parts of the community that are especially sensitive to pollutants, the mosses and the lichens. Despite reductions in pollution levels (and especially in sulphur) we found that the sensitive tree dwelling lichens had not made a full recovery in Sweden. Looking at sites across Europe we also found that moss communities had changed with nitrogen deposition, with shifts towards the species that cope well with high nutrients, and a loss in diversity. Finally, we used a method of putting a number on the stability of a site to track changes over time and see if these could be explained by pollution effects. While the extreme disturbances at the site in Paper I could be clearly seen, the pollution effects we saw in the most sensitive parts of the community in Papers II and III were too subtle to move the community as a whole.

Populärvetenskaplig sammanfattning

Du har antagligen hört talas om ”surt regn”, som var en enorm fråga redan på 1970- och 80-talet (och fortfarande finns i vissa delar av världen). Svavelutsläppen från industri, trafik och andra källor reste långa sträckor vilket föll tillbaka till jorden som surt regn, och skadade sjöar och skogar. Till skillnad från några av de miljöfrågor som vi står inför idag fanns det snabbt och effektivt internationellt samarbete för att lösa problemet och svavelutsläppen minskade snabbt. Även om detta var en framgångssaga, märkte forskarna att svavel inte var det enda problemet. Kväve släpptes också ut av trafik och jordbruk och kunde resa långa sträckor innan den kom tillbaka till jorden. Och medan svavelhalterna hade sjunkit kraftigt så minskade kvävehalterna inte like mycket. Kväve är ett gödningsmedel, vilket låter som en bra sak men som kan orsaka många problem. Det normala tillståndet för de flesta skogar är att kväve är en bristresurs, och många växter har evolverat för att klara låga nivåer av det. Att plötsligt ha stora mängder tillgängligt kan betyda att dessa växter får svårt att överleva, antingen för att för mycket kväve är direkt skadligt eller för att andra växter som föredrar höga nivåer av kväve utkonkurrerar dem. Denna typ av förändringar kan få allvarliga konsekvenser för mångfalden av växter och de djurarter som är beroende av dem och för de viktiga funktioner och tjänster som skogarna erbjuder oss.

I europeiska skogar finns det relativt få olika trädarter, och större delen av växtens biologiska mångfald finns i gräset, örterna, buskarna, mossorna och lavarna. Eftersom träd i allmänhet lever länge kan det ta många årtionden innan effekterna av föroreningar kan ses. Däremot kan vi se förändringar i skogsbottens vegetation mycket snabbare, så det var där vi tittade i dessa studier. Det kan vara viktigt att titta på vad som händer med en viss växtart, men i naturen existerar de inte isolerat. De interagerar alltid med andra arter på komplexa sätt, så vi pratar om växtsamhället, och det här samhället är där vi letade efter bevis på förändringar.

Förutom att undersöka om föroreningar orsakade förändringar i dessa samhällen, var vi också intresserade av hur mycket störningar de kan hantera. Här pratar vi om två närbesläktade begrepp, ekologisk stabilitet (hur väl ett ekosystem kan återhämta sig efter störningar) och ekologisk motståndskraft (hur mycket störningar systemet kan absorbera utan att bli ett fundamentalt annorlunda ekosystem).

I Paper I tittade vi på en svensk skog som drabbades av både en allvarlig storm och ett utbrott av träddödande barkbaggar. Det verkade möjligt att den kunde ändras från att vara mest gran till att bli en bokskog. Vi fann att även om vegetationen har förändrats mycket i de störda områdena, fanns det vissa områden som hade undgått det mesta av skadan. Dessa hjälpte gran och andra arter att rekolonisera och fungerade som "ekologiskt minne", vilket antyder att denna skog var motståndskraftig mot till och med extrema störningar (åtminstone på lång sikt). I Paper II och III fokuserade vi på två delar av samhället som är särskilt känsliga för föroreningar, mossorna och lavarna. Trots minskade föroreningsnivåer (och särskilt i svavel) fann vi att de känsliga trädboende laverna inte hade återhämtat sig helt i Sverige. När vi tittar på platser över hela Europa fann vi också att mossamhällen hade förändrats med kvävedeposition, med förskjutningar mot de arter som klarar höga näringsämnen och en reduktion i mångfalden. Slutligen använde vi en metod för att sätta ett nummer på webbplatsens stabilitet för att spåra förändringar över tid och se om dessa kan förklaras av föroreningar. Medan de extrema störningarna på platsen i Paper I tydligt kunde ses, var de föroreningar som vi såg i de mest känsliga delarna av samhället i Paper II och III för subtila för att flytta samhället som helhet.

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