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Vegetation community change in Atlantic oak woodlands along a nitrogen deposition gradient☆

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A B S T R A C T

Atlantic old sessile oak woodlands are of high conservation importance in Europe, listed in the European Union (EU) Habitats Directive Annex I, and known for their rich bryophyte communities. Their conservation status ranges from unfavourable to bad across their known distribution, which is predominantly within the UK and Ireland, but also extends into Iberia and Brittany. The objectives of this study were to determine if nitrogen (N) deposition, a known driver of terrestrial biodiversity loss, was a significant predictor of community composition in old sessile oak woodlands (i.e., EU Habitats Directive Annex I class: 91A0), and to identify significant changes in individual plant species and community-level abundance (i.e., change points) along an N deposition gradient. Relevé data from 260 Irish oak woodland plots were evaluated using Canonical Correspondence Analysis (CCA) and Threshold Indicator Taxa ANalysis (TITAN). Nitrogen deposition accounted for 14% of the explainable variation in the dataset (inertia = 0.069, $p < 0.005$). A community scale change point of 13.2 kg N ha^{-1} yr^{-1} was indicated by TITAN, which falls within the current recommended critical load (CL) range for acidophilous *Quercus*-dominated (oak) woodlands (10–15 kg N ha^{-1} yr^{-1}). The results suggest that the current CL is sufficient for maintaining a core group of indicator species in old sessile oak woodlands, but many nutrient sensitive species may disappear even at the CL range minimum.

1. Introduction

Old sessile oak woodlands with *Ilex* and *Blechnum* occur in the Atlantic region of Europe, predominantly within the United Kingdom and Ireland, although their range may extend into Brittany and north-west Iberia. These woodlands are dominated by *Quercus robur*, *Quercus petraea*, *Betula pendula*, and *Betula pubescens*, and are characterised by base-poor soils, high rainfall, and rich bryophyte assemblages. They are highly fragmented and have been placed on the European Union Habitats Directive (European Commission, 2015a) Annex I list because of their high conservation importance, but are nonetheless listed as having unfavourable or bad conservation status across their entire range (JNCC, 2013). The main threats to the stability of this habitat include land-use management, grazing, invasive non-native species, and air-borne pollutants.

It is widely accepted that loss of biodiversity has detrimental impacts on ecosystem structure, function, and services (summarized in Cardinale et al., 2012), and there is growing evidence that elevated nitrogen (N) deposition is a major driver of biodiversity loss in natural terrestrial ecosystems, ranked closely behind land-use and climate changes (Sala et al., 2000). Nitrogen is typically the limiting nutrient in terrestrial ecosystems (Tamm, 1991; Aerts and Chapin, 2000); as such, elevated N deposition has been shown to cause changes to plant community composition by influencing competitive interactions between species (summarized in Bobbink et al., 2010). Deposition gradient studies have shown decreases in plant species richness (Huang, 2012; Maskell et al., 2010; Stevens et al., 2004), reductions in oligotrophic species (Dirnbock et al., 2014), and increases in acid-tolerant species (Stevens et al., 2010a), all correlated with increasing N deposition. Globally, emissions of atmospheric reactive N (which includes oxidised, reduced inorganic species and organic N compounds, but excludes unreactive N_2 gas) from anthropogenic sources are estimated to have increased more than 12-fold between 1860 and 2005, and emissions are predicted to rise (Galloway et al., 2008).

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While habitat pressures such as land-use management, grazing, and invasive non-native species are routinely assessed under Article 17 reporting of the EU Habitats Directive, the impacts of N deposition are not explicitly addressed.

The critical load (CL) approach has been widely used in Europe to assess the negative impacts of elevated N deposition and support emissions reduction regulations (Bobbink and Hettelingh, 2011). There are two general approaches to setting CLs, i.e., using steady-state nutrient mass-balance models or empirical approaches (CLRTAP, 2004). Empirical approaches incorporate information from experimental N addition trials, supplemented with results from gradient or transect studies, to estimate the exposure below which significant harmful effects on specified sensitive elements of the environment do not occur. This approach has been used to set CL for nutrient N (i.e., reduced and oxidised N deposition leading to eutrophication) for sensitive habitat types across Europe under the United Nations Economic Commission for Europe's (UNECE) Convention on Long-range Transboundary Air Pollution (CLRTAP). The CLs for nutrient N have primarily focused on changes in biodiversity. However, it is recognized that the sensitivity of different ecosystems to elevated N deposition is highly variable and that further work is needed to causally relate N deposition to species diversity loss (Bobbink and Hettelingh, 2011).

There are many studies that suggest elevated N deposition negatively impacts grassland plant biodiversity (Clark and Tilman, 2008; Henry and Aherne, 2014; Maskell et al., 2010; Stevens et al., 2010a, 2010b, 2011a, 2011b). In contrast, few studies have evaluated the impacts of N deposition on plant communities in sessile oak woodlands. Previous studies of oak woodlands suggest that excessive N deposition may cause decreases in mycorrhiza (Nilsson et al., 2007), reduction of epiphytic lichens and bryophytes (Mitchell et al., 2004, 2005), and changes in ground vegetation (Brunet et al., 1998; Falkengren-Grerup and Diekmann, 2003). The current recommended empirical CL for nutrient N for *Quercus*-dominated (oak) woodland is 10–15 kg N ha^{-1} yr^{-1}, based on expert judgement and supported by seven gradient and re-sampling studies pertaining mainly to biodiversity losses or changes, and in one case to soil changes (Bobbink and Hettelingh, 2011).

The objective of this study was to assess the potential influence of N deposition on plant community structure in old sessile oak woodlands. This was carried out by using: (1) canonical correspondence analysis (CCA) to assess the relative importance of N deposition in determining community composition compared to climate and soil chemistry, and (2) Threshold Indicator Taxa ANalysis (TITAN; Baker and King, 2010) to identify individual species and overall community-level change in taxa abundance across a gradient in N deposition (to inform empirical CL's for nutrient N). TITAN detects abrupt changes in individual species' distribution along an environmental gradient; points at which a significant distributional change occurs are referred to as change points. A community-level change point is inferred where the majority of individual taxa change points converge. Ellenberg Indicator Values (EIVs; Ellenberg, 1979) were used to explore potential mechanisms behind observed community changes. Plant species data for 260 relevés from the Irish National Parks and Wildlife Service (NPWS) *National Survey of Native Woodlands* (NSNW) were utilized in this study. Recent estimates of reactive N deposition (Henry and Aherne, 2014; wet ammonium (NH_4^+) and nitrate (NO_3^-) plus dry NH_3 and N oxides (NO_x)) suggest that Irish Atlantic oak woodlands are distributed along a gradient in deposition that spans the current recommended CL range. Despite having high NH_3 emissions (ranking 9th among EU countries and exhibiting the highest intensity of NH_3 emissions per Gross Domestic Product (Henry, 2013)), Ireland receives relatively 'clean' Atlantic air and has low total NO_x emissions (ranking 20th in the EU), and in some regions total deposition is close to European background levels.

2. Methods

Study sites and vegetation survey data: Study sites were selected from woodland relevés surveyed under the NSNW, commissioned by the NPWS (URL: www.npws.ie). The survey was conducted by Botanical, Environmental and Conservation Consultants Ltd (BEC; URL: www.botanicalenvironmental.com). between 2003 and 2007 and included 1667 10 m $\times$ 10 m relevés in native woodlands across Ireland. At each relevé, vascular and bryophyte plant species abundance was recorded using the DOMIN scale (which ranges from simple presence through ten classes of linked cover-abundance; Mueller-Dombois and Ellenberg, 1974); in addition, notable lichens, soil pH, organic matter as loss-on-ignition (LOI), soil total phosphorous (P), soil type, stand structure, and natural regeneration were recorded (see Perrin et al., 2008 for NSNW detailed site selection, survey, soil sampling and data analysis methods). The relevés were classified into four vegetation groups (1. *Quercus petraea – Luzula sylvatica*, 2. *Fraxinus excelsior – Hedera helix*, 3. *Alnus glutinosa – Filipendula ulmaria*, and 4. *Betula pubescens – Molinia caerulea*) and 22 subgroups using multi-variate techniques. A list of plant species that were indicative of each vegetation group and subgroup were identified using Indicator Species Analysis (Dufrene and Legendre, 1997), which selects species based on their relative abundance between groups and relative frequency within groups.

All relevés classified under the *Quercus petraea – Luzula sylvatica* group ($n = 260$) were selected for this study. The ten key indicator species of this group were: *Quercus petraea*, *Luzula sylvatica*, *Isothecium myosuroides*, *Ilex aquifolium*, *Blechnum spicant*, *Vaccinium myrtillus*, *Lonicera periclymenum*, *Polypodium vulgare*, *Mnium hornum*, and *Rhytidiadelphus loreus*. The *Quercus petraea – Luzula sylvatica* group comprised three vegetation subgroups: 1. *Rubus fruticosus – Corylus avellana*, 2. *Vaccinium myrtillus – Ilex aquifolium*, and 3. *Luzula sylvatica – Dryopteris dilatata*. While the NSNW classification system was a vegetation classification system, not a habitat classification, 99% of the *Quercus petraea – Luzula sylvatica* group were considered analogous to the Annex I habitat type 'Old sessile oak woods with *Ilex* and *Blechnum* in the British Isles' (EU Code 91A0). Study sites were located in 23 of the 26 Irish counties; however, the majority of the sites were located in the east and south of the country (Fig. 1).

Plant species abundance data for each relevé were obtained in Turboveg format (Hennekens and Schaminee, 2001); species richness was calculated for each relevé under Turboveg (based on the total number of species rather than the number of species minus those identified as negative indicators, e.g., invasive species). While change in species richness does not necessarily describe all aspects of biodiversity change, i.e., a count of the number of species does not describe the species composition or necessarily reflect ecosystem health, nonetheless, it is a widely used indicator of such (e.g., Maskell et al., 2010; Mitchell et al., 2005; Payne et al., 2011; Stevens et al., 2010b). As such, it was chosen for initial exploratory analysis to direct variable selection for further statistical analysis, i.e., only variables correlated with species richness were used in CCA.

2.1. Spatial datasets

Mapped long-term (1981–2010) mean annual temperature and annual rainfall data were obtained from Met Éireann (2014) on a 1 km $\times$ 1 km grid. Long-term (1991–2010) total N deposition (wet NH_4^+ and NO_3^- plus dry NH_3 and NO_x for forests) maps were