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Plant and vegetation functional responses to cumulative high nitrogen deposition in rear-edge heathlands

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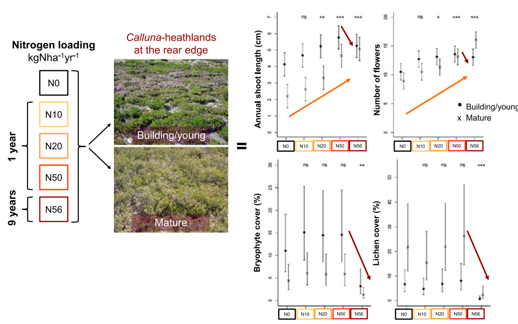
HIGHLIGHTS

- The annual growth and flowering of *Calluna* plants responded positively to N addition.
- Young plants showed early signs of N saturation under cumulative (9-year) N loading.
- There were no significant N-driven changes in plant species composition and richness.
- Mosses and lichens cover declined only with cumulative N at both young/mature heaths.
- Marginal *Calluna*-heathlands are thus moderately resistant to cumulative high-N inputs.

GRAPHICAL ABSTRACT



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ABSTRACT

Elevated atmospheric nitrogen (N) deposition is a major driver of change, altering the structure/functioning of nutrient-poor *Calluna vulgaris*-heathlands over Europe. These effects amply proven for north-western/central heathlands may, however, vary across the ecosystem's distribution, especially at the range limits, as heathlands are highly vulnerable to land-use changes combined with present climate change. This is an often overlooked and greatly understudied aspect of the ecology of heathlands facing global change. We investigated the effects of five N-fertilisation treatments simulating a range of N deposition rates (0, 10, 20, and 50 kg N ha^{-1} yr^{-1} for 1 year; and 56 kg N ha^{-1} yr^{-1} for 9 years) on the *Calluna*-plants, the plant functional groups, species composition and richness of two life-cycle stages (building/young- and mature-phase) of *Calluna*-heathlands at their rear-edge limit. Our findings revealed a dose-related response of the shoot length and number of flowers of young and mature *Calluna*-plants to the addition of N, adhering to the findings from other heathland locations. However, cumulative high-N loading reduced the annual growth and flowering of young plants, showing early signs of N saturation. The different plant functional groups showed contrasting responses to the cumulative addition of N: annual/perennial forbs and annual graminoids increased with quite low values; perennial graminoids were rather abundant in young heathlands but only slightly augmented in mature ones; while bryophytes and lichens strongly declined at the two heathland life-cycle stages. Meanwhile there were no significant N-driven changes in plant species composition and richness. Our results demonstrated that *Calluna*-heathlands at their low-latitude distribution limit are moderately resistant to cumulative high-N loading. As north-western/central European heathlands under high-N inputs broadly experienced the loss of plant diversity and pronounced changes in plant species dominance, rear-edge locations may be of critical importance to unravel the mechanisms of heathland resilience to future global change.

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1. Introduction

Human activities have exceedingly increased the mobility and deposition of biologically reactive forms of nitrogen (N) in recent decades worldwide (Galloway et al., 2004, 2008; Peñuelas et al., 2017). This anthropogenic disruption of the global N cycle is responsible for biodiversity loss and altered ecosystem processes in a great variety of terrestrial ecosystems (e.g., Bobbink et al., 2010; Ochoa-Hueso et al., 2011). What is more, cumulative N inputs are one of the most significant factors producing unprecedented changes in the functioning of ecosystems, even at low deposition rates (Clark and Tilman, 2008; De Schrijver et al., 2011; Humbert et al., 2016; Phoenix et al., 2012). Understanding the magnitude of the effects of long-term airborne N depositions is, therefore, of major importance for the preservation of ecosystems, in particular, semi-natural habitats adapted to low levels of N availability (Field et al., 2014; Humbert et al., 2016; Phoenix et al., 2012; Soons et al., 2017; Stevens et al., 2016).

Heathlands dominated by the dwarf shrub *Calluna vulgaris* (L.) Hull (henceforth referred to as *Calluna*) are semi-natural ecosystems on nutrient-poor soils pertaining to traditional cultural landscapes within Atlantic Europe (Loidi et al., 2010), highly endangered across their entire distribution range (Fagúndez, 2013). Land-use changes (abandonment or intensification), N pollution, natural succession, and invasion by exotic species are the main drivers causing heathland habitat destruction and fragmentation throughout Europe (e.g., Bartolomé et al., 2005; Britton et al., 2017; Henning et al., 2017; Rose et al., 2000). Many heathland field-surveys and N-manipulation experiments over different temporal scales have strongly demonstrated that elevated N deposition leads to (1) changes in plant growth, phenology and chemistry (e.g., Bähring et al., 2017; Britton and Fisher, 2008), (2) increased plant sensitivity to abiotic/biotic stressors (e.g., Heil and Diemont, 1983; Prins et al., 1991), (3) a reduction in plant diversity (Britton and Fisher, 2007; Maskell et al., 2010; Southon et al., 2013), (4) the loss of N-sensitive plant species (Caporn et al., 2014; Van den Berg et al., 2008), and (5) the invasion by nitrophilous species (Britton and Fisher, 2007; Southon et al., 2013). Moreover, a few long-term researches demonstrated the lasting nature of the majority of these N-driven impacts on the heathland ecosystem (Carroll et al., 1999; Field et al., 2017; Power et al., 2006; Southon et al., 2012) that are expected to continue over coming decades (Payne et al., 2017; Stevens et al., 2016). These studies, however, have principally been accomplished in north-western and central European *Calluna*-heathlands; very little is known about the responses of southern heathlands at the rear-edge of the ecosystem's distribution to elevated N availability (Calvo et al., 2005, 2007; Cuesta et al., 2008; Marcos et al., 2003), especially over the long-term (Calvo-Fernández et al., 2018; Taboada et al., 2016). This lack of knowledge impedes the implementation of proper on-site management to counterbalance the potentially detrimental impacts of N loading in rear-edge heathland locations that are also vulnerable to present climate change (Fagúndez, 2013). Whereas for other heathland areas across Europe, diverse management measures (e.g., grazing, mowing, prescribed burning, sod-cutting; Härdtle et al., 2009; von Oheimb et al., 2009) have been tested for their effectiveness in maintaining the low-nutrient status of the given heathland location with minor adverse impacts on the ecosystem (see review by Jones et al., 2017).

Recent researches have shown that environmental factors affect species differentially at the centre and the edges of their distribution ranges (e.g., Pearson et al., 2009; Viejo et al., 2011; see review by Sagarin et al., 2006), with notable dissimilarities between leading and rear edges (i.e., high- and low-latitude limits, respectively; Hampe and Petit, 2005). This generally implies that findings from a given location within a species' range might not be applicable to other parts of the range (Sagarin et al., 2006). Within the broad distribution area of *Calluna*-heathlands across Europe, it is very likely that dominant *Calluna* plants from different locations have evolved particular adaptive traits to their local conditions (Loidi et al., 2010) and are, thus, differentially sensitive to environmental changes. To our knowledge, though, only one study (Meyer-Grünefeldt et al., 2016) has experimentally assessed how central and marginal *Calluna* plants responded to global change testing the single and combined effects of drought and N deposition. This study concluded that (1–2-year-old) plants from the southern-most limit of the *Calluna*-heathland ecosystem's distribution are better adapted to drought events than those from the centre of the range, except under elevated N availability. It is, however, difficult to extrapolate the results of these short-term effects on potted *Calluna* seedlings to long-term effects on more complex natural systems. Further research is, therefore, necessary to investigate the differential resistance of *Calluna*-heathlands across the entire distribution range to shifting environments under global change.

Here, we evaluate the impact of different doses of N loading (0, 10, 20, and 50 kg N ha^{-1} yr^{-1} for 1 year, and 56 kg N ha^{-1} yr^{-1} for 9 years) on the functioning of *Calluna*-heathlands at their southern-most distribution limit by assessing the responses of two life-cycle stages of *Calluna*-heathland development: building/young (9-year-old plants) and mature (30–40-year-old) growth phases (Gimingham, 1972). To date, there are only a few studies testing how age affects heathland responses to N deposition (Caporn et al., 2014; Jones and Power, 2015; Meyer-Grünefeldt et al., 2015, 2016); this is despite contrasting plant growth rates and vegetation structures among heathland life-cycle stages (i.e., pioneer, building, mature and degenerate phases; Gimingham, 1972). Specifically, we examine how increased N inputs alter the annual growth and flowering of *Calluna*, the different plant functional groups (annual/perennial forbs and graminoids, woody species, bryophytes and lichens), and plant species composition and richness. According to prior findings from north-western and central European heathlands, we hypothesised that experimentally-increased N availability in rear-edge heathlands will result in: (i) enhanced *Calluna*-plant productivity (Bähring et al., 2017; Britton and Fisher, 2008; Southon et al., 2012) especially at the building stage due to higher plant growth rates and nutrient demand (Jones and Power, 2015); (ii) a shift in plant species composition towards more nitrophilous plant communities (Britton and Fisher, 2007; Southon et al., 2013) with higher relative abundances of graminoid species (Bobbink and Heil, 1993; Friedrich et al., 2011; Prins et al., 1991); and (iii) a decline in plant species richness (Maskell et al., 2010; Southon et al., 2013) associated to the loss of N-sensitive species (Caporn et al., 2014; Van den Berg et al., 2008) such as bryophytes and lichens (Bähring et al., 2017; Pilkington et al., 2007), particularly with cumulative (9-year) N inputs (De Schrijver et al., 2011).

2. Material and methods

2.1. Study area

The study was conducted in three *Calluna* heathland sites (San Isidro, Riopinos I, and Riopinos II) located in the Cantabrian Mountains (NW Spain; 43°02–03′N, 5°21–26′W; 1560–1660 m a.s.l.; 18–35 ha in size) [see Calvo-Fernández et al., 2018 for additional information] included as priority habitat type in Annex I of the Habitats Directive (92/43/ECC; habitat code 4060: alpine and boreal heaths). The climate is Eurosiberian (total precipitation of 1308 mm and mean temperature of 7.0 ± 4.9 °C during the study year 2014) with a brief and moderate drought period in July–August, and a snow cover duration from late-autumn until the end of May. Soils are Umbrisol characterised by high acidity (pH = 3.9 ± 0.14; deionized water), low fertility, sandy texture and high permeability (Marcos et al., 2009). The vegetation growing season comprises from May to October and the bud burst of *Calluna* plants happens in June. The three sites are subjected to minimal regular free-range grazing by cattle and horses (1–2 LU ha^{-1} yr^{-1}) in June–September. Total N deposition in the study area ranges from 7.5 to 15 kg N ha^{-1} yr^{-1}, according to the EMEP and CHIMERE models for