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A nitrogen index to track changes in butterfly species assemblages under nitrogen deposition

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ABSTRACT

The impacts of nitrogen deposition (N) on animal communities are still poorly understood in comparison to plant communities. Long-term monitoring of community changes may contribute to this understanding, complementing experimental studies on underlying mechanisms. Butterflies are particularly suitable for such analyses, because the different species cover a broad gradient of productivity, their ecological traits are well-known, monitoring data are available in a growing number of countries, and the short life history of butterflies ensures a rapid response to changing environmental conditions.

Here, we use species-specific nitrogen optima to develop a community nitrogen index (CNI) for butterflies in the Netherlands. Over a 25-year period (1990–2015), data from the Dutch Butterfly Monitoring Scheme reveal a significant increase in the CNI in response to high nitrogen deposition levels. However, the rate of increase is declining, in close parallel with reduced nitrogen deposition loads. The continuing increase indicates that nitrogen deposition still exceeds the critical nitrogen load of butterfly communities in the Netherlands. Overall, the relative increase of butterflies from more productive environments reflects the advantage, under high nitrogen availability, of mobile and multivoltine species with high reproductive capacity, rapid larval development and hibernation as pupae or adults. We discuss the perspectives and limitations in applying the CNI at both national and local scales. We propose that, when taking the critical nitrogen load of the examined butterfly community into account, the CNI may prove a valuable tool to track changes of biotic communities in relation to nitrogen deposition.

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1. Introduction

Anthropogenic deposition of reactive nitrogen (N) from agriculture, traffic and industry is considered as one of the main drivers of current biodiversity loss and change of ecosystem functioning besides changes in land use and climate (Vitousek et al., 1997; Sala et al., 2000; Naeem et al., 2012; Ceballos et al., 2015). The excessive input of reactive N has even been ranked as a major threat to ecological stability at a global level (Rockström et al., 2009; Steffen et al., 2015). Although its impacts have been mainly studied in parts of Europe and North America, the worldwide increases in N deposition render it a phenomenon of global importance (Erisman et al., 2013). With respect to terrestrial biodiversity, research has focused on the effects of N deposition on plant communities (Tamis et al., 2005; Van Landuyt et al., 2008; Stevens et al., 2010; Bobbink et al., 2010). Evidence of the impact of N deposition on animal communities is scarce, however, and largely restricted to insects (Maes and Van Dyck, 2001; Pöyry et al., 2016; Nijssen et al., 2017).

Insects comprise a large share of the world's biodiversity and fulfil an important role in terrestrial nutrient cycling (Weisser and Siemann, 2004). Nitrogen addition experiments have shown trophic cascades in insect communities, with biomass of herbivores and detritivores increasing but parasitoid abundance decreasing with plant biomass (Haddad et al., 2000). Raised N contents in plant tissue may lead to a greater frequency of insect pest outbreaks (Throop and Lerdau, 2004). However, insect species richness was shown to decline with N addition, particularly in herbivore and parasitoid species (Haddad et al., 2000). Possible mechanisms causing these N-driven changes in community structure are discussed in more detail by Nijssen et al. (2017). Studies of butterfly communities in temperate climates suggest that these are affected by increasing levels of reactive N mainly through the cooling of microclimates (WallisDeVries and Van Swaay, 2006), loss of herbaceous hostplants (Weiss, 1999; Tamis et al., 2005; Bobbink et al., 2010) and nectar sources (WallisDeVries et al., 2012; Lebeau et al., 2016), as well as alterations in hostplant quality (Fischer and Fiedler, 2000; Turlure et al., 2013; Audusseau et al., 2015; Nijssen et al., 2017).

In the context of conservation of biological diversity, it is not only crucial to gain understanding of driving mechanisms but also to develop

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indicators to track the impact of N excess on biodiversity (Dale and Beyeler, 2001). Such indicators should give information on global and regional biodiversity trends in relation to N deposition, but should also be able to indicate the effectiveness of local measures to mitigate its impacts. When coupled to information on species traits, indicator changes also provide insights into changes in community structure (WallisDeVries, 2014). Community indices have been developed for temperature in the context of climate change (Devictor et al., 2008, 2012a). For temperature, the index response may be expected to respond in direct proportion to temperature change as a result of changes in relative abundance of species with warm or cool temperature optima, albeit with possible time lags (Devictor et al., 2012a, 2012b). For N, we hypothesize that the response of a community nitrogen index (CNI) is more complex. With an increasing N load, the response should follow direct proportionality as for temperature, but with a decreasing N load the response should vary in dependence of the critical N load (see Bobbink et al., 2010 for a discussion of the concept). If levels of N deposition exceed critical levels for a particular community, a decrease in deposition should still lead to an increasing CNI value, as long as the deposition exceeds the critical N load. Only when N deposition falls below the critical load, should this also result in a decrease of the CNI. Under a scenario of N deposition reduction, the rate of CNI increase will be positive above the critical N load but gradually decrease with diminishing exceedance. Only when N deposition drops below the critical load, will the increase turn into a decrease; and at a growing rate with continued reduction in N deposition. Thus, it should be informative to track the rate of change in the CNI besides its actual value. However, due to time lag effects of ecosystem functioning to changes in N deposition (Stevens, 2016), it could well be that even the response of organisms with the rapid population turnover of insects will be slow or erratic.

Here, in addition to the plant-based metrics proposed by Rowe et al. (2017), we present a CNI based on abundance changes in butterfly communities from northwestern Europe. Butterflies are particularly suitable for such analyses, because different species cover a broad gradient of productivity (Oostermeijer and Van Swaay, 1998; Feest et al., 2014), their ecological traits are well-known (WallisDeVries, 2014; Eskildsen et al., 2015), monitoring data are available in a growing number of countries (Van Swaay et al., 2008), and the short life history of butterflies, with at least one generation per year, ensures a rapid response to changing environmental conditions (Thomas, 2005). This rapid response could provide a major advantage over indicators based on the slower response of species composition change in plant communities (Rowe et al., 2017). We apply the CNI at the national scale in the Netherlands and compare it to the trend in N deposition. We test if the annual change in CNI was correlated with the N deposition in the preceding year, i.e. the minimum response time for a butterfly community. We then investigate how this CNI reflects the traits of contributing species. Finally, we discuss possible limitations and explore the potential application of the index to monitor change at small spatial scales.

2. Material and methods

2.1. Community nitrogen index

In building a community nitrogen index (CNI), we followed the procedure adopted by Devictor et al. (2008, 2012a) to develop a community temperature index for birds and butterflies and built on the N index used by Feest et al. (2014). The CNI reflects the relative contribution of high- versus low-N organisms in local communities. The N value of each species was derived from the optimal Ellenberg N values for the plant communities in which a species is recorded with highest occupancy, as assessed for the Netherlands by Oostermeijer & Van Swaay (1998; Table A.1) on the basis of butterfly and vegetation data on sites from the Dutch Butterfly Monitoring Scheme over the period 1992–1994. The CNI of a local community then is the average N value of recorded species, weighted by their abundances.

We calculated a yearly CNI for the Netherlands from the monitoring transects of the Dutch Butterfly Monitoring Scheme for the period 1990–2015. In this scheme, butterfly numbers of all species are counted on a weekly basis between April 1st and September 30th along permanent transects under suitable weather conditions (details on methods in Pollard and Yates, 1993). Each transect consists of a series of usually 20 sections of 50 m length and 5 m width. The transects are distributed over the whole country (494 transects with at least 8 years of observations); imbalances in geographical distribution are accounted for in species trend analyses by a weighting procedure according to six main soil regions (dunes, sea clays, lowland peat, river clays, Pleistocene sands and calcareous soils) and six habitat types (woodland, heathland, agricultural land, moorland, dunes and urban areas) (Van Swaay et al., 2002). Species counted in <10 transects and transects counted in a single year were excluded from the analysis. The irregular migrant *Vanessa cardui* was also excluded, because its abundance is mainly determined by factors outside the Netherlands (Stefanescu et al., 2013)

Yearly species abundances on each transect were calculated by applying a generalized additive model (GAM) to repeated counts within monitoring sites across the Netherlands (following Schmucki et al., 2015). Linear trends of CNI in time were determined by standard least squares linear regression with site as a random factor; a quadratic year factor was added to test for a curvilinear response.

We correlated the predicted annual change in CNI to annual values of reactive N deposition in The Netherlands for preceding year for the period 1990–2014. Predicted annual changes in CNI were used besides observed changes to filter out the noise from yearly variation. Nitrogen deposition data were obtained as summed deposition of reduced and oxidised N in mol ha^{-1} year^{-1} from RIVM (2015; www.clo.nl/nl018914).

2.2. Species traits, status and nitrogen affinity

We focused on 56 resident butterfly species in the Netherlands (Table A.1). Nitrogen indicator values were derived for most species by Oostermeijer and Van Swaay (1998) on the basis of species occupancy probabilities as a function of Ellenberg N values for vegetation relevees along butterfly monitoring transects. Butterfly species were then grouped in four groups of different N affinity (after Tamis et al., 2005): low (N-optimum <4), average (N-optimum 4–6), high (N-optimum ≥6) or indifferent (no significant relation with N value).

Species traits were analysed on the basis of trait components from WallisDeVries (2014). Using trait components instead of separate traits has the advantage that the components are mutually independent, whereas many individual traits are closely correlated. Thus, each species was characterised by its score on four principal trait components, reflecting (1) spatial use and reproductive capacity (contributing variables: population area, vagrancy, wing size, potential egg production), (2) climatic conditions (contributing variables: hardiness, moisture, temperature), (3) generation time (contributing variables: larval growth rate, voltinism, overwintering stage, diapause flexibility), (4) resource specialisation (contributing variables: territorial behaviour, food plant specialisation, oviposition behaviour).

Species responses were included as Red List status in ordinal categories after WallisDeVries (2014) and as the slope of log-transformed abundance trends over the long-term (1992–2014) and over a more recent period (2004–2014). Abundance data were again obtained from the Dutch Butterfly Monitoring Scheme (see Section 2.1); for *Phengaris alcon, Lycaena dispar* and *Thecla betulae* trends in abundance are derived from egg counts in plots of a known size (typically 100 m²).

Trait differences between N affinity groups were tested by a non-parametric Kruskal-Wallis test, because of inhomogeneity of variances. For tests on species status, we distinguished only two N classes (N-sensitive: low-average N values vs. N-tolerant: high-N or indifferent),