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RESEARCH ARTICLE

Nitrogen Deposition Increases Spontaneous Forest Establishment and Loss of Lichen Vegetation in Inland Dune Areas Across the Netherlands

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ABSTRACT

Questions: (1) How much of the inland dune habitat has been transformed into spontaneous forest across the Netherlands between 2007 and 2018? (2) Is there a spatial correlation between nitrogen deposition and changes in vegetation? (3) What changes could be observed in the cover of lichen vegetation and the invasive bryophyte *Campylopus introflexus* within this period? (4) What measures can be taken to counteract the effect of spontaneous forest establishment?

Location: Inland dune sites across the Netherlands are primarily located in the eastern part of the country.

Methods: Comparative analysis of vegetation maps made in 2007 and 2018. Lichen species trends were estimated based on a study with 75 permanent plots over the period 1999–2023.

Results: Our study shows that, with increasing N deposition, the spontaneous forest establishment rate doubles. The Netherlands loses 118 ha (0.7%) of inland dune vegetation to spontaneous forest establishment annually, which is largely compensated by nature restoration measures. Increasing nitrogen deposition causes a stronger dominance of *Campylopus introflexus*. This resulted in a 40% decrease in the abundance of terrestrial lichen species, and consequently in a decrease in overall habitat quality.

Conclusions: N deposition has a positive effect on spontaneous forest establishment in inland dune areas across the Netherlands. In total, site management would have to fell a minimum of 118 ha of Scots pine annually as a restoration measure to combat the spontaneous establishment rate and maintain the current open area inland dune habitat. Habitat quality was negatively affected and visible as a strong decline in lichen abundance and an increase in the invasive moss *Campylopus introflexus*.

1 | Introduction

During the last ice age, large parts of the Netherlands, Northern Germany, Poland and surrounding areas became covered in aeolian sand deposits, the so-called European sand belt (Koster 1978). These cover sands were believed to be vegetated with forest and heather up to the Middle Ages. Deforestation and overexploitation, like intensive sheep grazing, sod cutting and uncontrolled burning of the heathland, made the landscape susceptible to wind erosion, which resulted in the formation of inland dunes that reached their maximum size in the middle of the 19th century. At that time, most of the inland dune sites that now remain were much larger drift sand areas with no vegetation at all (Castel et al. 1989; Castel 1991). Starting from the late 19th century, Scots pine (*Pinus sylvestris*) was planted at a large scale in inland dune areas and heathlands to support the wood and mining industry (Koster 2005; Riksen et al. 2006). As a result, the total area of drift sand—bare sand with sparse or no vegetation—has decreased from 80,000 ha around 1850 to 4000 ha in 1980 in the Netherlands (Riksen and Jungerius 2010). This decrease in drift sand area continued between 1950 and 2007, as shown by a more detailed study by Sparrius et al. (2013). During this period, the forest area increased within the Netherlands. As spontaneous forest on inland dunes becomes older, its biodiversity value increases (Prach et al. 2021).

Inland dunes are internationally recognised under the European Habitats Directive (Council Directive 1992) and protected within the network of Natura 2000 sites. Inland drift sands harbour Natura 2000 habitat types 2330 (Inland dunes with open *Corynephorus* and *Agrostis* grasslands), which include drift sands. Other low vegetation is formed by later successional stages classified as 2310 (Dry sand heaths with *Calluna* and *Genista*) and the rare habitat type 2320 (Dry sand heaths with *Calluna* and *Empetrum nigrum*). Further successional stages consist of forests dominated by Scots pine or oak (*Quercus robur*), which do not fall under a Natura 2000 habitat type.

Semi-natural landscapes, such as inland dunes, need conservation measures to survive. Events with wind erosion became rare and less intense as this requires large open areas, which have now disappeared (Riksen et al. 2006). Afforestation of Scots pine by man may have stopped; however, the existing trees produce large numbers of seedlings, resulting in spontaneous forest development (Riksen et al. 2006; Ujházy et al. 2011; Prach et al. 2021). Nitrogen deposition and climate change further increase the speed at which later successional stages are formed and provide better growing conditions for the invasive bryophyte *Campylopus introflexus*, which causes a reduction of lichen cover due to competition for space (Sparrius et al. 2011; Essl et al. 2014). Critical loads for N deposition in inland dune vegetation and heathland were estimated to fall within 5 and 15 $kg\,ha^{-1}\,yr^{-1}$ (357–1071 $mol\,ha^{-1}\,yr^{-1}$) (Bobbink et al. 2022). However, N deposition exceeds these levels in most Natura 2000 sites (CBS et al. 2022).

To counteract the effects of (increased) succession, the three most applied conservation measures are (1) sod cutting to restore drift sands and allow bare sand to become vegetated with early successional grasses, bryophytes and lichens; (2) removal of tree seedlings to prevent sites from becoming a forest; and (3) restoration of open inland dune habitat by forest removal, often followed by sod cutting. Extensive grazing by deer and sheep may further slow down vegetation succession or divert succession towards heathland instead of forest (Riksen et al. 2006).

The habitat area of all inland dunes in the Netherlands, and the habitat quality of eight sites were mapped by Sparrius et al. (2013) in 2007. In 2018 (and partly 2020), we updated the habitat map, revisiting the same eight sites to analyse which changes in area of the successional stages of inland drift sands and habitat quality had occurred. With this new data, we are able to answer the following research questions:

1. How much inland dune habitat has been transformed into spontaneous forest across the Netherlands in the period 2007–2018?
2. Is there a spatial correlation between nitrogen deposition and changes in vegetation?
3. What changes could be observed in the cover of lichen vegetation (positive quality indicator) and the invasive bryophyte *Campylopus introflexus* (negative indicator) between 2007 and 2020?
4. What is the required scale of the measures that should be taken to counteract the effect of spontaneous forest establishment in sites with low and high N deposition?

By answering these questions, we aim to quantify the effect of nitrogen deposition on spontaneous forest establishment in inland dune areas and the implications for management.

2 | Methods

2.1 | Study Area

Inland dune soils were mapped by Riksen and Jungerius (2010) by drawing polygons on a combination of the Dutch soil map and a relief-shaded map based on altimetry maps. One hundred and twenty-seven sites were identified, and the accuracy of the polygon boundaries is <10 m. Within these sites, eight smaller sites were selected within a nitrogen deposition gradient for mapping by Sparrius et al. (2013). Throughout the area, 75 permanent plots were located for lichen monitoring (e.g., van der Kolk and Sparrius 2023).

Regions are suitable for comparison as they lie a maximum of 150 km apart in the Atlantic ecoregion. They have similar annual precipitation levels and temperatures (Heijboer and Nellestijn 2002). With a shared origin of aeolian cover sands, soil mineralogy shows a high similarity between sites (Sparrius 2011).

2.2 | Mapping Changes in Sand, Open Area and Forest Cover

Sparrius et al. (2013) created a vegetation map for eight different inland drift sand reserves by interpreting aerial photographs in the years 1954, 1981, 1995 and 2007. The vegetation was classified as either 'sand', 'open' or 'forest'. 'Sand' meaning bare drift sands with no vegetation, 'open' meaning pioneer vegetation and 'forest' meaning closed forests or large solitary trees. For this study, we expanded the 2007 maps to inland dunes in the entire country and repeated the method for the situation in 2018. This has been done using the following steps in QGIS 3.26 (QGIS Development Team 2022):

1. A detailed topographical map of the Netherlands (scale 1:10,000 of the years 2007 and 2018) (pdok.nl/datasets: Top10NL) was clipped by the contour map of inland dunes.
2. Terrain types were combined into sand, open (heathland) and forest. Roads, built-up areas and water bodies were removed from the maps. Sliver polygons and gaps < 1 m were removed.
3. Eight large sites were mapped in more detail using high-definition aerial photographs with a resolution of 10 cm/pixel (pdok.nl/datasets: 'luchtfoto'). Additionally, aerial imagery for selected sites was made using an AgEagle eBee X fixed-wing drone with an RGB camera. Photographs were georeferenced and classified with eCognition Developer into the classes sand, open vegetated area and forest. The resulting maps were pasted into the 2007 and 2018 maps.
4. Topographical maps tend to show even irregular forested areas at a very high precision; however, contours of bare sand were less precise. Therefore, larger patches of bare sand were checked and corrected by hand for sites where we did not use automated classification.
5. The 2007 and 2018 maps were then combined ('union' operator), resulting in almost 200,000 polygons with their habitat in both years. A data column was added with the interpretation of changes in successional stages. These are classified as 'loss of sand' and 'spontaneous forest establishment' (forward succession), 'sod cutting' and 'felling' (reverse succession indicating restoration measures) or none in case the successional stage remained the same.

The area of the successional stages and their changes is equal to the sum of the area of the corresponding polygons.

2.3 | The Relation Between Forest Establishment and Nitrogen Deposition

To visualise the spontaneous forest establishment, the polygons with the classification 'open area' in 2007 and 'open area' or 'forest' in 2018 were selected. This selection was then unioned with a 1 km grid (Sparrius 2022). The change in forest cover was calculated for each km square as the percentage of open area that had become forest in 2018, resulting in a value between 0% (no forest establishment) and 100% (all open area was transformed into forest). Each square was attributed to the 2018 map with modelled average nitrogen deposition at the same spatial resolution (RIVM 2019). Grid cells with fewer than 5 ha of forested area were removed from the dataset.

The N deposition was categorised in five classes (< 1300, 1300–1500, 1500–1700, 1700–1900 and > 1900 mol $ha^{-1} yr^{-1}$), and the mean change in forest cover, standard error and sample size were calculated using R (Appendix S1). The data were not normally distributed (Shapiro–Wilk test; $p < 0.05$), so we applied the non-parametric Kruskal–Wallis test to examine the differences between multiple groups. Following this, a Dunn (Bonferroni method) post hoc test was used to analyse which specific groups differed.

2.4 | Changes in Lichen and *Campylopus* Cover

To determine changes in sand dune quality, we compared lichen and *Campylopus* cover between 2007 and 2020. The eight sites studied in 2007 by Sparrius et al. (2013) were revisited using the same survey method. During 10 days of fieldwork, 40 ha were mapped by walking through the sites and drawing vegetation types on an aerial photograph by hand, as remote sensing techniques were not found to be reliable for this aim. This resulted in maps for each area showing where high (> 25%) cover of lichens or the bryophyte *Campylopus introflexus* occurred. Further data analysis consisted of calculating the cover of both vegetation types for each site for those parts of the sites that were open vegetated areas in both survey years.

2.5 | Changes in Lichen Species Occupancy and Abundance

In 1999, a lichen monitoring network was established in inland dunes in the Netherlands. Permanent plots of typically 100–500 m^2 were surveyed every 5 years, and all lichen species were recorded together with their abundance (Aptroot and Sparrius 2002). Plots were subdivided into 10 subplots, and the abundance was estimated as the proportion of subplots in which the species was observed, in the following classes: 0, 0.1, 0.2–0.5 and 0.6–1. Proportion data cannot be analysed using conventional regression analysis. Therefore, we applied a beta regression model, which is capable of analysing proportion data observed within class boundaries (Irvine et al. 2016), resulting in species index values per 5-year period. These were converted into index values with the value of the first period set at 100. Thereafter, the species index values were averaged geometrically to produce Multi-species indicator values (MSI; Soldaat et al. 2017). The calculation of the MSI accounts for sampling error of species indices by taking into account the confidence intervals of the species index values. Trends in the MSI were statistically tested by estimating the percentage change between the values of the last period and that of the first period. The percentage change is significant if its confidence interval does not include 0. Similarly, differences between MSIs were tested by estimating the difference in trend and associated confidence intervals (Soldaat et al. 2017). The following lichen species were included in the list of larger species: *Cetraria islandica*, *Cladonia arbuscula*, *C. furcata, C. portentosa, C. scabriuscula, C. gracilis, C. uncialis and C. zopfii*. Smaller lichens included *Cetraria aculeata*, *Cladonia* species with cups or squamules (e.g., *Cladonia borealis, C. cervicornis, C. coccifera, C. foliacea, C. strepsilis* and others) and the crustose lichen species *Baeomyces rufus, Diploschistes muscorum, Placynthiella* spp. and *Stereocaulon condensatum*. Larger species often form thick cushions between grasses, whereas smaller species reach a maximum height of 2 cm and grow directly on mineral soil or humus. Apart from abundance trends, species occupancy trends and MSIs were calculated by only taking into account the presence of a species in a plot.

3 | Results

A sample map and changes between years are shown in Figure 1. The full map is provided as open data (Sparrius 2019).

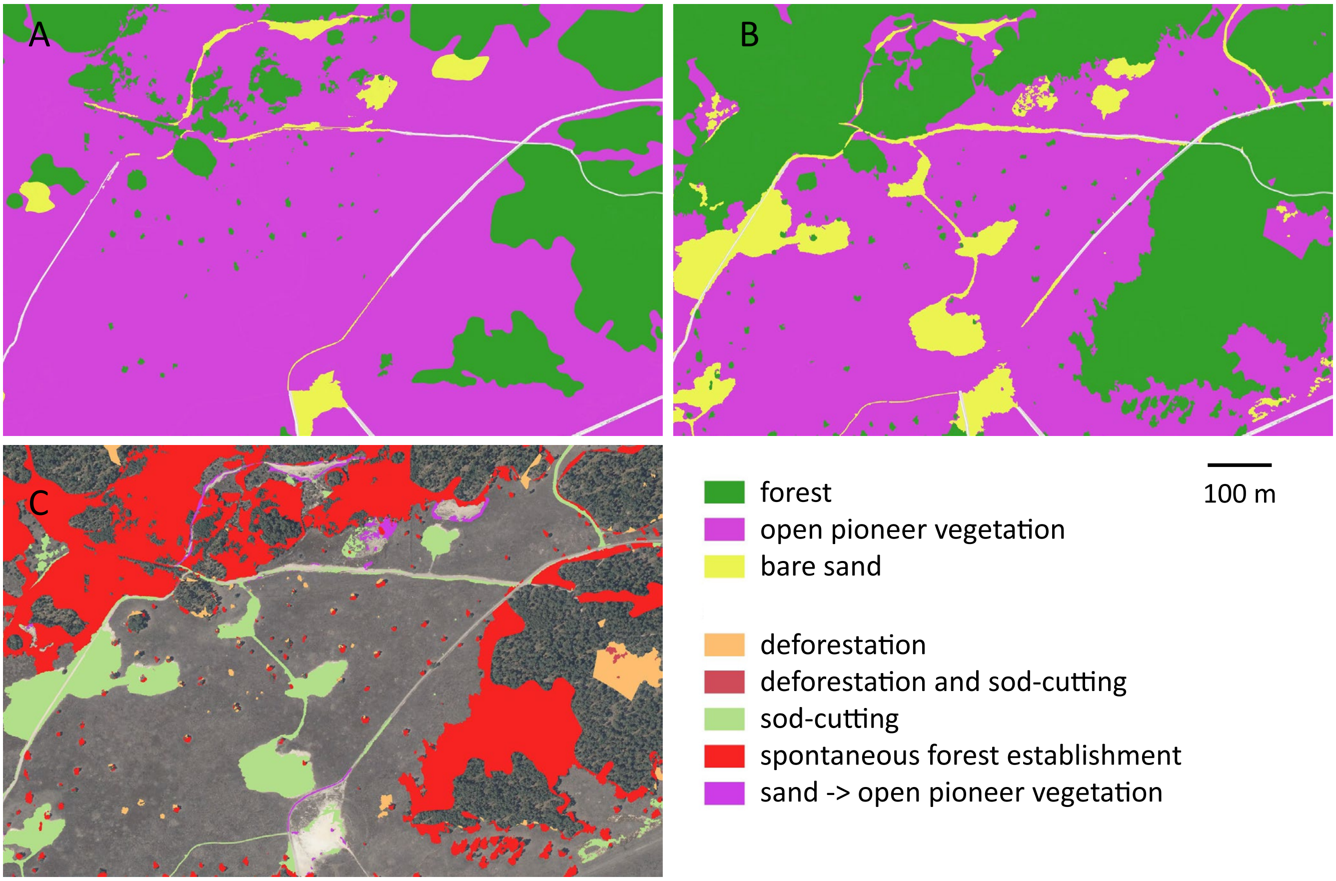

FIGURE 1 | Example cut-outs of the vegetation maps (A) 2007, (B) 2018 and (C) the changes on an aerial photograph. Site: Otterlose Zand. Map data is in a Zenodo repository. Aerial photograph: Kadaster.

TABLE 1 | Area (in ha) bare sand, pioneer vegetation and forest on inland dune soil inside and outside Natura 2000 sites in the Netherlands in 2018.

Sites	Bare sand	Pioneer vegetation	Forest	Total
Natura 2000 sites	1440	9872	27,249	36,562
Outside Natura 2000 sites	259	4920	24,586	29,765
Total	1699	14,792	51,835	66,327

Note: Based on the map shown in Figure 1.

3.1 | Changes in Inland Dune Vegetation Between 2007 and 2018

Pioneer vegetation and bare sand are part of the EU protected habitat types 2330, 2310 and 2320 and are therefore largely found within Natura 2000 sites. Bare sand forms about 11% of these three inland dune habitat types (Table 1).

Over the period 2007–2018, about 6% of the area showed a change in vegetation class (Table 2). On average, 37 ha of bare sand was lost annually, but restoration measures created 33 ha, resulting in a net loss of only 3 ha per year. Spontaneous forest establishment caused the loss of 118 ha of pioneer vegetation per year. However, 206 ha of new pioneer vegetation was created by natural succession on bare sand (37 ha) and by cutting forest (169 ha).

3.2 | Effect of Nitrogen Deposition on Spontaneous Forest Establishment

Spontaneous forest establishment rate was higher in areas with higher levels of nitrogen deposition. Differences were significant between the lowest and highest groups (Figure 2). Forest establishment varied from 7% (for the lowest class $< 1300\,\mathrm{mol\,N\,ha^{-1}\,yr^{-1}}$) to 16% (for the highest class $> 1900\,\mathrm{mol\,N\,ha^{-1}\,yr^{-1}}$).

3.3 | Changes in Lichen and *Campylopus introflexus*–Dominated Vegetation

Between 2007 and 2020, the invasive bryophyte *Campylopus introflexus* increased in cover in the eight study areas. In the four low N deposition sites, the cover of the area where the species was dominant was low and slightly increased to 4% of the total pioneer vegetation cover. In the four high N deposition sites, *Campylopus* cover was much higher and substantially

TABLE 2 | Changes in bare sand, pioneer vegetation and forest inside and outside Natura 2000 sites in the Netherlands in 2007 compared to 2018.

Sites	Sand to pioneer vegetation	Pioneer vegetation to forest	Pioneer vegetation to sand (sod cutting)	Forest to Sand (deforestation and sod cutting)	Forest to open pioneer vegetation (deforestation)	No change
Natura 2000 sites	238	884	224	97	1190	33,931
Outside Natura 2000 sites	169	413	23	29	672	28,458
Total	407	1297	247	126	1862	62,389
Total per year	37	118	22	11	169	

Note: Areas are given in hectares.

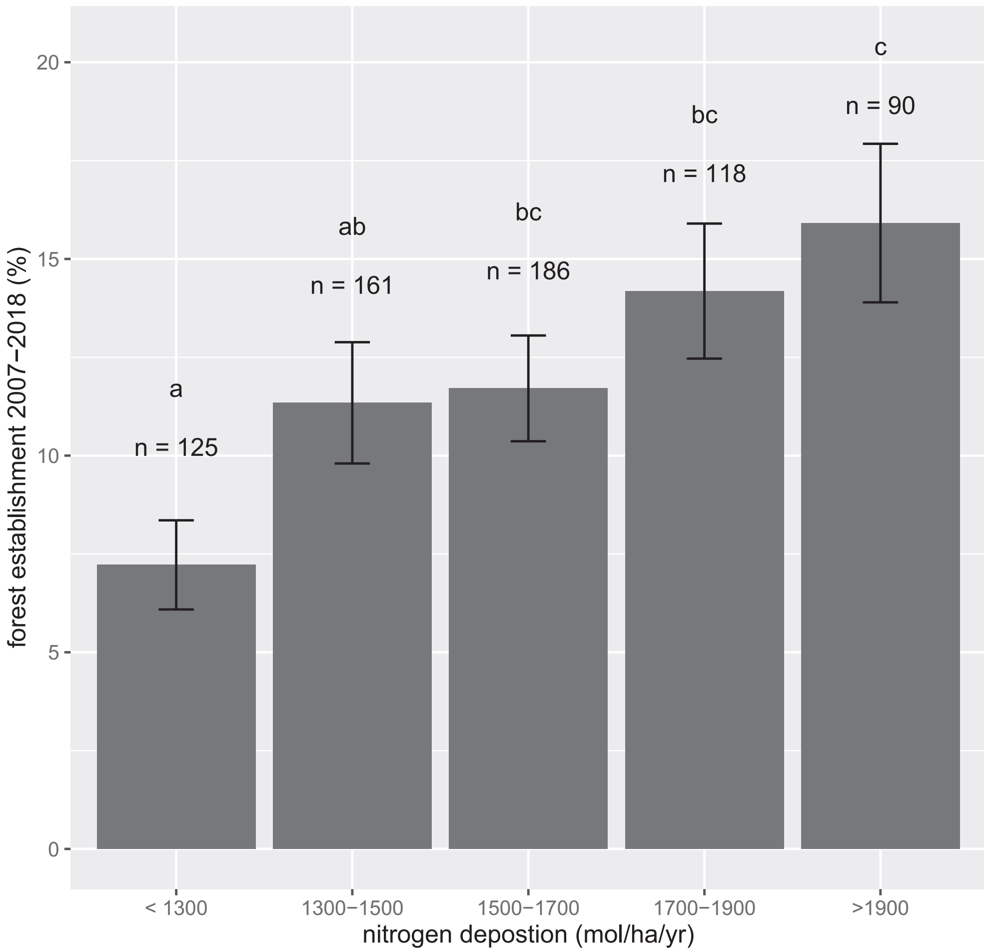

FIGURE 2 | The percentage of open area transformed into forest in 1 km squares between 2007 and 2018 differentiated between N deposition classes. Different letters indicate significant differences between groups (Kruskal–Wallis test, $p < 0.05$). For primary data, see Appendix S2.

increased to 60% of the total area (Table 3). Regarding lichen cover, the changes were small, with similar low cover percentages in sites with low and high N deposition (Table 3). Lichens increased at one site with high N deposition (Wekeromse Zand), where large-scale restoration measures were taken in 1994. Changes between years were not significant (paired *t*-test), but *Campylopus*-dominated vegetation was significantly higher in sites with high N deposition (unpaired *t*-test; $p = 0.005$).

3.4 | Changes in Lichen Occurrence and Abundance in Permanent Plots

We obtained trends for 35 lichen species, of which 16 were significantly negative. No species increased in abundance. The MSI, an abundance index for all species together, declined from index value 100 (in 1999–2003) to 60 (in 2019–2023), indicating a 40% decline. Some lichen species showed a stronger decline than others. The time series of lichen species abundance showed a decline, with smaller species being the most affected (Figure 3). This difference was significant (paired t-test; $p<0.05$). Larger lichens were reduced by about 25%, whereas smaller species dropped by 55%. Among the most affected lichen species were *Cladonia macilenta* (−52%), *Stereocaulon condensatum* (−45%) and *C. glauca* (−39%). No species showed a significant increase.

For 34 species, separate trends for high (> 1800 mol ha^{-1} yr^{-1}) and lower N deposition sites could be compared. The trend in occupancy was significantly more negative in high N deposition sites (paired t-test; $p=0.02$). The trend in abundance showed a similar pattern; however, it was not significantly different (paired t-test; $p=0.07$).

TABLE 3 | Cover and standard deviation of vegetation dominated by lichens and *Campylopus introflexus* in 2007 and 2020 in eight sites in sites above and below the median value of the nitrogen deposition in the study areas.

Vegetation	Cover (%) in 2007	Cover (%) in 2020
Sites with N deposition < 1800 mol N ha^{-1} yr^{-1} ($n=4$)		
Campylopus introflexus	2 ± 2	4 ± 8
Lichens	8 ± 5	7 ± 5
Sites with N deposition > 1800 mol N ha^{-1} yr^{-1} ($n=4$)		
Campylopus introflexus	37 ± 39	60 ± 23
Lichens	6 ± 5	10 ± 9

Note: For primary data, see Appendix S4.

4 | Discussion

4.1 | Vegetation Succession

Annually, 118 ha of spontaneous forest is established in inland dunes (Table 2). Also, 33 ha of bare sand is transformed into pioneer vegetation, a number that falls within the range estimated from historical data (1950–1995) by Sparrius et al. (2013).

4.2 | Effect of Nitrogen Deposition on Succession

The results show that, with increasing N deposition, the mean spontaneous forest establishment rate increases (Figure 1). Sites with higher N deposition are therefore more vulnerable to habitat loss.

Inland dunes in the Netherlands receive far more N deposition than the average critical load of 714 mol ha^{-1} yr^{-1} calculated by Bobbink et al. (2022). This means that even low deposition sites compared in this study receive 3 to 4 times more N than the upper limit for healthy ecosystem functioning. Experimental N addition on lichen vegetation in high N deposition sites resulted in increased N:P ratios in common inland

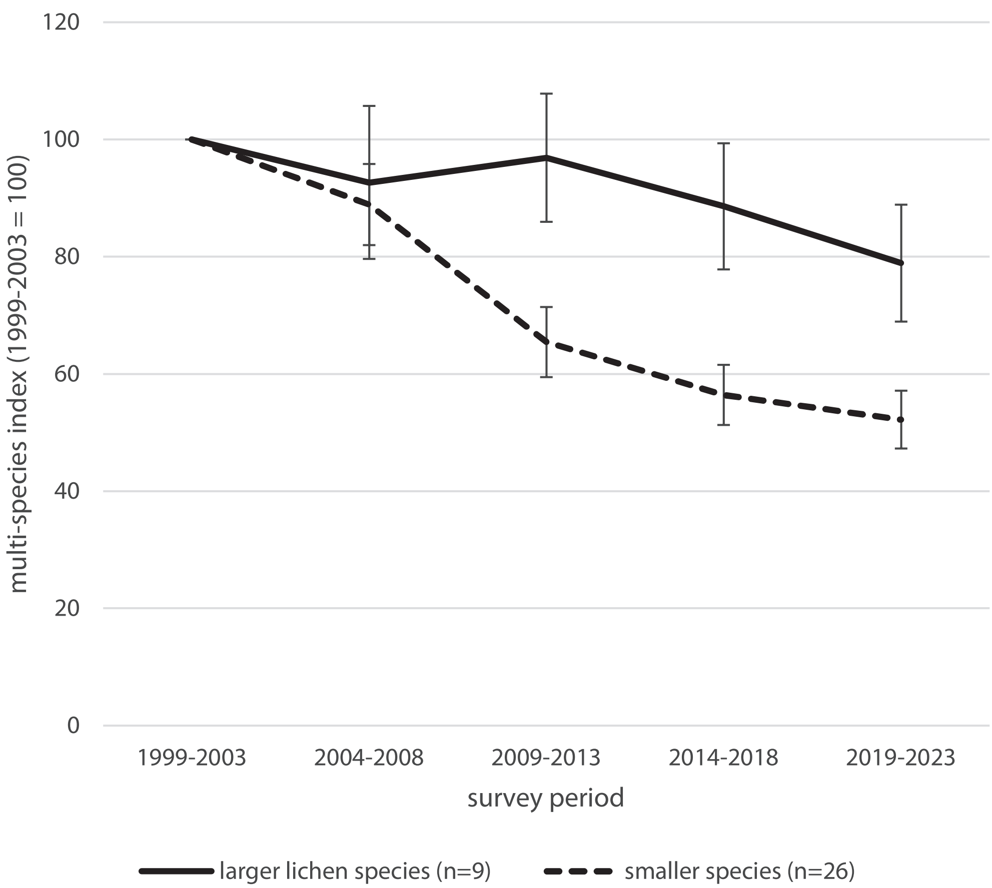

FIGURE 3 | Multi-species abundance trends of smaller and larger lichens in 75 inland dune plots. For primary data, see Appendix S3.

dune grasses and the lichen *Cladonia portentosa*, but not in biomass production, suggesting that other nutrients than N are limiting growth (Sparrius and Kooijman 2013). In Natura 2000 sites receiving high levels of N deposition, such as the Veluwe area, the N deposition will have to decrease, as the current restoration efforts are not sufficient to compensate for habitat loss (Sparrius et al. 2021).

4.3 | Effects of Nitrogen Deposition on Habitat Quality

The invasive moss *Campylopus introflexus* increased in cover in all sites, but remained low in sites with lower N deposition. The cover of lichen-dominated vegetation showed little change, except for one site where it started to increase 25 years after restoration measures were taken (Ketner-Oostra 2003). Sparrius and Kooijman (2011) estimated that *Campylopus introflexus* became invasive in a rather devastating way at deposition levels above 2100 mol N ha^{-1} yr^{-1}, but our study shows that N levels should be at least below 1800 mol to avoid *Campylopus* dominance. This corresponds with a study in moorland sites in Britain where *Campylopus introflexus* frequency started to strongly increase at nitrogen deposition levels above 1500 mol N ha^{-1} yr^{-1} (Caporn et al. 2014). Competition by *Campylopus introflexus* has also been observed by Mikulášková et al. (2012) in acidic grasslands with lichens in the Czech Republic.

Despite the small change in cover of lichen-dominated vegetation, many lichen species showed a strong overall decrease in abundance. This negative trend was especially visible in smaller species as compared to larger lichens. This can partly be explained by succession, as larger lichens occur in *Calluna* heaths and taller vegetation dominated by *Agrostis vinealis*, rather than in more recently colonised sand dunes. However, survey plots were large enough to harbour a mosaic of vegetation types and bare sand. Presumably, smaller lichens were not able to colonise new locations in high N deposition sites. Sparrius and Kooijman (2011) already showed that this might be caused by competition with *Campylopus introflexus*, as sites with high N deposition show a higher *Campylopus*:lichen ratio in freshly colonised sites. Other studies have shown that competition by moss, grass and shrub encroachment plays an important role in the decline of lichen-dominated vegetation in open natural areas or forest understories. In the case of Canadian tundra, He et al. (2024) showed that disturbance by wildfires and also, presumably, climate change caused a decline in lichen cover. A long-term study in the Fennoscandian tundra by Vuorinen et al. (2017) showed a shift from a lichen-rich tundra towards an ericoid-moss tundra, attributed to climate change.

4.4 | Restoration Efforts

When comparing lost habitat due to spontaneous forest establishment and realised restoration effort, targets to preserve the area of Natura 2000 habitat types are met at a national scale. Furthermore, in our analysis, we found that restoration measures were carried out in equal proportions inside and outside Natura 2000 sites. Current N deposition and land use require this management to be continued indefinitely.

5 | Conclusions

Overall, the inland dune habitat area slightly increased, while habitat quality diminished. Without restoration measures, pioneer vegetation in inland dunes would transform into pine forest at a rate of 118 ha (0.7%) per year for the Netherlands. Restoration activities in the period 2007–2018 were sufficient to maintain and slightly increase the area of pioneer vegetation. Our study shows that sites receiving higher levels of atmospheric N deposition have higher spontaneous forest establishment rates, lower lichen cover, lower lichen diversity and higher cover and increase of the invasive bryophyte *Campylopus introflexus*.

Author Contributions

Laurens B. Sparrius conceived the research idea; Daniël Kollen, Laurens B. Sparrius, Michel J.P.M. Riksen and Michaël J. Duijsens collected the data; Laurens B. Sparrius, Michaël J. Duijsens and Arco J. van Strien performed the statistical analyses; Laurens B. Sparrius and Michaël J. Duijsens wrote the paper; all authors discussed the results and commented on the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Primary data used for the analysis of this research can be found in the cited Zenodo archives (https://zenodo.org/records/7640805, https://zenodo.org/records/5653903) and the cited maps in the Netherlands geo portal, pdok.nl. Primary lichen monitoring data are available upon request. Data for Table 3 and data and an R script to produce Figure 2 and statistical tests are given in the appendices.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.