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Experimental evidence for disturbance as key to the conservation of dune grassland

Ane Kirstine Brunbjerg [a,b,*], Jens-Christian Svenning [a], Rasmus Ejrnæs [b]

[a] Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, Ny Munkegade 114, DK-8000 Aarhus C., Denmark
[b] Wildlife Ecology and Biodiversity Group, Department of Bioscience, Aarhus University, Grenaavej 14, DK-8410 Rønde, Denmark

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ABSTRACT

Coastal dunes are dynamic systems maintained and renewed by disturbance. Concerns have been raised over shrub and tree encroachment, changes in species composition and decreasing species richness in coastal dunes with nitrogen (N) deposition and loss of natural dynamics acknowledged as pressures. We tested the effects of N-deposition and disturbance on Danish dune grassland vegetation. We applied simulated trampling, grazing, blowouts and N-deposition in a randomized design to ten sites along the major natural gradient in the area. After three years we recorded plant, bryophyte and lichen biomass as well as species frequency, foliar N and P, soil pH and soil organic matter content. We hypothesized that species richness would increase with disturbance and decrease with N-addition while biomass was expected to increase with N-addition. Disturbance was expected to counteract the effects of N-addition. The hypotheses were tested using linear mixed effects models on species richness, biomass and phylogenetic community structure with treatments and interactions among treatments as explanatory variables and site as a random effect. Although N-deposition affected plant nutrient balance, the effect of N-addition on vegetation was consistently smaller than the effect of disturbance, especially cutting. Disturbances all had the opposite effect to N-addition causing an increase in species richness and decrease of biomass. The subordinate effect of N-addition likely reflects that growth is limited by moisture rather than nitrogen. Disturbances apparently relaxed the ecological filtering during community assembly, resulting in a more diverse community of less related species. Anthropogenic suppression of disturbances by wind, coastal erosion or grazing animals may potentially be a larger threat to dune biodiversity than increased N-deposition.

1. Introduction

Humans have been attracted to coastal areas for millennia, exploiting different resources (e.g., fishery, fuel wood, construction material, shipping) as well as settling in the areas, cultivating them and more recently using them for recreation, tourism and military training (Everard et al., 2010; UNEP, 2006). Still, coastal landscapes are often controlled by natural processes (e.g., Kumler, 1993) and have high conservation value compared to many inland ecosystems. Therefore, national and international conservation legislation initiatives have been proposed to protect near-natural coastal ecosystems against further anthropogenic pressures (UNEP, 2006).

Dunes comprise an important part of coastal ecosystems and the mosaic-like vegetation structure is maintained primarily by strong, natural processes such as strong winds, sand deposition and coastal erosion (Maun, 2009; Warming, 1909). The outcome is a directional successional gradient from bare sand over species-poor pioneer communities to species-rich herb communities and finally towards leached and stabilized dunes with species-poor dwarf-shrub heath (Maun, 2009). From an evolutionary perspective dune vegetation is adapted to recurrent disturbances (Brunbjerg et al., 2012a) and without these shrubs and trees will eventually invade with loss of typical dune species (Aptroot et al., 2007).

Over longer time scales, coastal dune formation and persistence is related to climatic variability as well as exploitation causing a sparser and less resistant vegetation cover. Cold periods have caused more severe storms and this in turn has renewed the coastal dune habitats because of increasing sand mobilization (Clarke and Rendell, 2011; Provoost et al., 2011). Throughout

* Corresponding author. Tel.: +45 87 15 88 65, mobile: +45 60 62 32 97.
E-mail addresses: anekirstinebrunbjerg@gmail.com (A.K. Brunbjerg), svenning@biology.au.dk (J.-C. Svenning), rej@dmu.dk (R. Ejrnæs).

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European history, utilization of dune plants for building materials, utensils etc. as well as livestock grazing intensified the disturbance regime in coastal dunes (Jensen, 1994; Plassmann et al., 2010; reviewed in Provoost et al., 2011). During the last century these disturbances have diminished or ended. Furthermore, initiatives to prevent sand drift (e.g., establishment of dune plantations, planting of *Ammophila arenaria* L. Link) to protect agricultural areas, infrastructure and habitations within the last 100–200 years have led to dune stabilization (Gilbertson et al., 1999; Jensen, 1994; Provoost et al., 2011).

Over the past 70 years nitrogen (N) deposition caused by burning of fossil fuels, increasing density of livestock and use of manure may also have had an effect on dune vegetation (Bobbink et al., 2011). Critical N loads for dune grassland have been estimated to be 8–15 kg N ha^{-1} $year^{-1}$ (Bobbink et al., 2011) and despite recent decreases in N loads (EMEP, 2010), current N-deposition in most western European countries is within or above this range. N-deposition has been found to increase biomass and decrease species richness in fixed coastal dunes and grasslands (e.g., Jones et al., 2004; Stevens et al., 2004). Furthermore, N-deposition potentially changes community composition as eutrophication and acidification may cause selective local extinction of sensitive species (Greven, 1992; McClean et al., 2011).

The interaction of disturbance and productivity has been shown to play a key role in community assembly and the maintenance of species diversity in local plant communities (Ejrnæs et al., 2006; Huston, 1994). It is argued that disturbances such as grazing and sand drift may mitigate the negative effects of N-deposition by limiting vigorous plant growth and creating gaps for re-colonization of subordinate species (Bakker and Olff, 2003; Jutila and Grace, 2002). Disturbance may affect not only species composition, but also phylogenetic community structure. Thus, disturbance has been found to cause phylogenetic clustering in ploughed fields as compared to abandoned fields (Dinnage, 2009), i.e. species in disturbed areas are more closely related than expected by chance due to shared phylogenetically conserved traits contributing to disturbance tolerance. Furthermore, clustering has been found to be the most pronounced phylogenetic signal in coastal dunes in Denmark and linked to anthropogenic disturbances (Brunbjerg et al., 2012a). We therefore expect that disturbance will change species composition and increase richness as well as the relatedness of species in the community.

In this study we examined the effect of N-addition and disturbance on species diversity, composition and productivity in a controlled field experiment along a natural ecological gradient in dry dune grassland Denmark. The study habitat is a priority habitat of the European Habitats Directive (European Commission, 2007) and knowledge about its vegetation responses to changes in nutrient availability and disturbance is paramount to its conservation. We hypothesized that the three types of disturbances (simulated grazing, trampling and blowouts) would cause an increase in species richness and reduce plant biomass while N-addition would cause a decline in species richness and an increase in plant biomass. Furthermore, species composition was expected to change in response to treatments.

2. Methods

2.1. Study site

Our study site was the near-natural, species-rich dune system "Tornby Klit" in Northern Jutland, Denmark (57°32′N, 9°54′E, Fig. 1). The study area is dominated by dry dune grassland on moderately calcareous sand with interspersed shrubs of *Salix* spp., *Hippophäe rhamnoides* L. and *Rosa* spp. Dominant plant species are *Poa pratensis* L., *Festuca arenaria* L., *Galium verum* L., *Plantago lanceolata* L., *A. arenaria* L. Link, *Hypnum cupressiforme* Hedw. and *Camptothecium lutescens* Hedw. Physical disturbance (e.g., wind, sand deposition) maintains the dunes and the effect is evident when comparing maps and photos from the last century (see Appendix A). Our study habitat corresponds to a calcareous or neutral subtype of "Fixed dunes with herbaceous vegetation (grey dunes)" (European Commission, 2007), hereafter referred to as dune grassland.

Due to the patchy nature of coastal dunes there is a trade-off between site area and site homogeneity. We settled on a site area of 10 m^2 and a plot size of 1 m^2 enabling the placement of treatments in relatively homogenous areas at the cost of relatively small buffer areas between neighbouring plots. Ten 2 m × 5 m experimental sites were randomly selected, but stratified to cover the primary vegetation gradient in Danish dunes to account for the possible effect of starting condition on the treatment response. Experimental sites were chosen randomly along the primary gradient in Danish dunes (for details see below and Appendix B). Despite the relatively small geographic distance between some sites (Fig. 1) they were considered as independent sites because of the high level of environmental heterogeneity and topographic variation in the study area (typical of coastal dunes). The experiment was established in June 2009 and treatments were repeated in August 2009, April/June/August 2010–2011 and April 2012, after which responses were recorded in August 2012.

2.2. Experimental setup and harvest

Each of the ten sites was divided into ten 1 m × 1 m plots with the following treatments applied (N-addition, freshwater addition (=control), blowout, N-addition + blowout, cutting, cutting + N-addition, trampling, trampling + N-addition, cutting + trampling and cutting + trampling + N-addition). Treatments were allocated randomly to each plot with the restriction that no treatment combination occupied the same position twice (across sites). The experiment was multifactorial, except that cutting and trampling were not combined with blowout. Because of the limited time for plants to respond to the treatments, nitrogen addition was augmented to two times the current N-deposition (imposed level equalled 30 kg N ha^{-1} $year^{-1}$) in the form of ammonium nitrate (NH_4NO_3) diluted in tap water (2.9 g L^{-1} m^{-2}) and applied using a watering can with sprinkler (1 L $plot^{-1}$). Untreated plots were watered with tap water (1 L $plot^{-1}$). Grazing was simulated by cutting the aboveground biomass to a height of two cm with removal of the biomass. Cattle trampling was simulated by pressing the end of a wooden pole (surface area 10 cm^2) with a pressure of approximately 1.5 kg/cm^2 into the sand 50 times per plot. This corresponds to the pressure of a cow trampling 5% of the plot area on three occasions during the growing season (Buttenschøn, 2007). We applied trampling and cutting separately to be able to disentangle their effects. The first trampling treatment in June 2009 was doubled (pressing 100 times per plot). Blowout (or heavy rooting by animals) was achieved by digging up all plants and their underground vegetative parts to a depth of 15–20 cm. The blowout treatment was not repeated. All treatments were applied to the plot (1 m × 1 m), while the response was measured only in the inner 0.5 m × 0.5 m area, leaving a buffer zone between plots with different treatments. In 2012 plot foliar C, N and P in grasses (primarily *F. arenaria* and *A. arenaria*) were determined (Appendix C), soil pH was measured and soil organic matter was estimated from soil samples by loss-on-ignition after combustion at 550 °C (Appendix C). Slope was measured in each plot and temperature and soil humidity loggers were installed in each site logging data every 30 min during May 2010.