



An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms

Niels M. Schmidt*, Jesper B. Mosbacher*, Palle S. Nielsen, Claus Rasmussen, Toke T. Høye and Tomas Roslin

N. M. Schmidt (nms@bios.au.dk), J. B. Mosbacher and P. S. Nielsen, Dept of Bioscience, Aarhus Univ., Roskilde, Denmark. C. Rasmussen, Dept of Bioscience, Aarhus Univ, Aarhus, Denmark. – T. T. Høye, NMS and JBM, Arctic Research Centre, Aarhus Univ., Aarhus, Denmark. TTH also at: Aarhus Inst. of Advanced Studies, Aarhus Univ., Aarhus, Denmark, and Dept of Bioscience, Aarhus Univ., Rønde, Denmark. – T. Roslin, Dept of Agricultural Sciences, Univ. of Helsinki, Finland, and Dept of Ecology, Swedish Univ. of Agricultural Sciences, Uppsala, Sweden.

Environmental monitoring aims to evaluate the state of nature, and to detect emerging threats (Lindenmayer and Likens 2009, Nie and Schultz 2012). Yet, the cautionary principle of science may hamper detection at the risk of reduced ecosystem health. Of particular concern are changes in the functioning of entire communities (Walther 2010), where potential consequences of change are devastating. Clear-cut indicators at the community-scale are, however, hard to derive. Here, we define an indicator of the community-wide scope and timing of pollen carrying capacity. We apply this measure to long-term monitoring data of High Arctic plants and pollinators to reveal that with current and future arctic warming, the timing of plant flowering and pollen transfer seems to be heading towards a functional disruption. By drafting this community-wide perspective on interaction phenology, we aim to direct attention to an impending functional disruption in the Arctic – and more broadly to stimulate functionally-oriented research into how ecosystems are responding to climate change.

Rapid climate change in the arctic regions is currently challenging organisms, processes and entire ecosystems there (Post et al. 2009). One likely consequence of the fast climatic change is the disruption of biotic interactions (Parmesan 2006, Settele et al. 2014). Indeed, observed phenological advancement at high latitudes is outpacing that at lower latitudes, with some indications of taxa-specific differences (Høye et al. 2007). While such reports are concerning, it is unclear to what extent ecological functions, such as pollination, may be at risk. To examine this, a community-wide, functional approach is needed. Community-wide time series and metrics of ecosystem services are however in short supply and the community-wide implications of phenological changes remain unclear.

Plant–pollinator interactions are among the most ecologically important relationships in nature, and are being

influenced by climate change (Hegland et al. 2009, Miller-Struttman et al. 2015). Several factors are important for the outcome of the plant–pollinator interaction, and factors such as the degree of synchrony between mutualistic partners, their abundances, visitation rates and pollen-carrying capacities are all critical for determining the rate of the interaction (Hegland et al. 2009, Petanidou et al. 2014, Forrest 2015). They should thus all be taken into account when examining the functional implications of phenological shifts.

The ongoing ecosystem-based monitoring at Zackenberg in High Arctic Greenland (Forchhammer et al. 2008) offers a unique opportunity to examine phenological plant–pollinator uncoupling at the community-scale during a period of rapid environmental change (Supplementary material Appendix 1, Fig. A1). Here, we extend previous analyses of temporal patterns in the flowering of plants and the abundance of the two most common families of Diptera (Høye et al. 2013), to include all 10 dominant groups in the local pollinator community (Rasmussen et al. 2013). By including data on pollen-carrying capacities of the respective taxa, we derive a functional measure of the full pollen-transport service (Supplementary material Appendix 1, Table A1).

As a measure of the pollen-transport capacity of the insect community, and the seasonal supply of this service, we weigh each taxon by the amount of pollen it carries. We then multiply taxon-specific abundance with pollen-transport capacity, thus achieving a metric of pollen transport available weekly through 18 growing seasons at Zackenberg (for details, see Supplement material Appendix 1). By comparing the timing of this service with the timing of flowering (Fig. 1a), we observe both to be highly but differently responsive to changes in climatic conditions (Supplementary material Appendix 1): hence, while the flowering season has become markedly shorter (–5.1 d per °C (Fig 1b); –8.5 d per decade (Supplementary material Appendix 1, Fig. A2)), the duration of the pollen transfer season has remained relatively stable with a slightly increasing trend (+ 2.6 d per °C

*Co-first authors

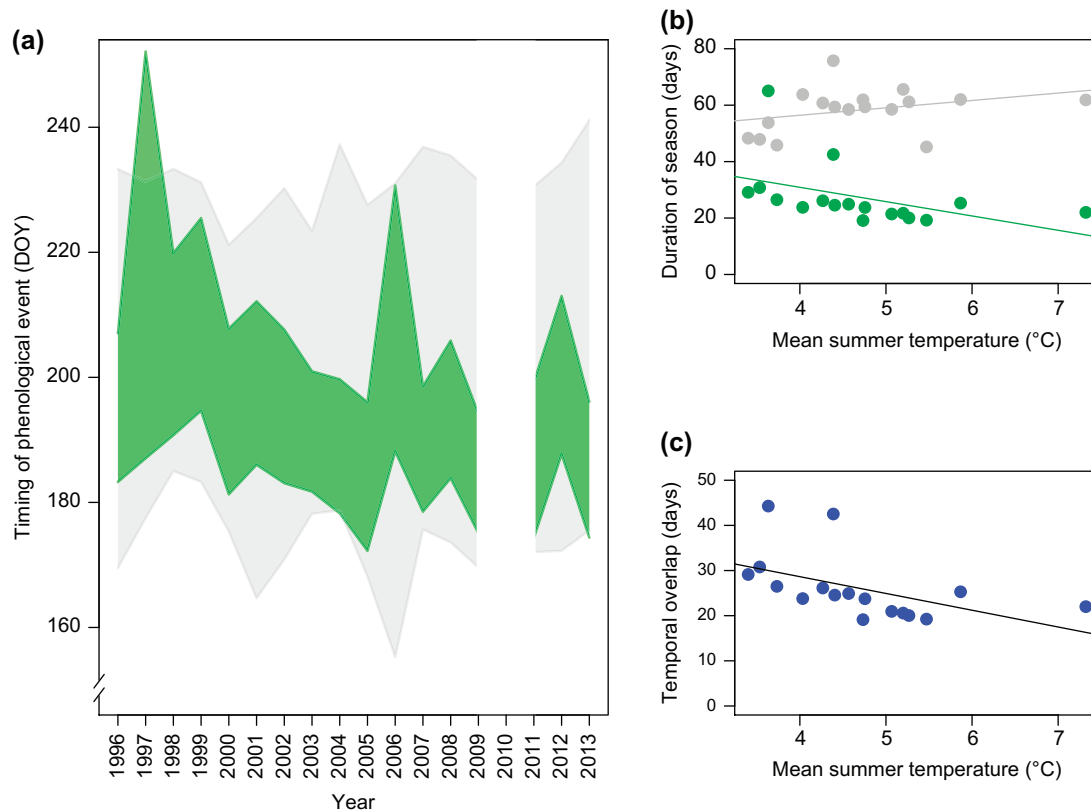


Figure 1. Community-wide phenological responses at Zackenberg, High Arctic Greenland, 1996 to 2013, showing (a) the duration of plant flowering (green) and pollen transfer season (grey) during the study period. DOY refers to the day of year after 1 January (data from 2010 are missing); (b) the duration of flowering (green) and pollen transfer season (grey) in relation to summer mean temperature, and (c) the temporal overlap between the flowering and the pollen transfer seasons in relation to summer mean temperature. Solid lines show significant trend lines ($p < 0.05$).

(Fig. 1b); +2.4 d per decade (Supplementary material Appendix 1, Fig. A2)). As the temporal overlap between the flowering season and the pollen transfer season is mainly determined by the flowering season (cf. Fig. 1a), the overlap is declining with current arctic warming (-3.7 d per $^{\circ}\text{C}$ (Fig. 1c); -5.4 d per decade (Supplementary material Appendix 1, Fig. A3)). The contrasting trends appear linked to abiotic drivers (i.e. significant interactions between response type and local temperature or timing of snow-melt; Supplementary material Appendix 1, Fig. A2). That the increasing temperature is an important mechanism behind the decreasing temporal overlap is strengthened by a further consideration: the relationship between year and temporal overlap is declining but to date only statistically non-significantly so (Supplementary material Appendix 1, Fig. A3), whereas the linkage between summer temperature and overlap is statistically detectable (Fig. 1c). Importantly, if temperature is a main driver, then the observed pattern is really the one to expect – as large year-to-year variation typical of the Arctic (cf. Supplementary material Appendix 1, Fig. A1) will weaken the relation to year per se in any finite series. These contrasting trends in the plant community and the pollinator function suggest that they are set for functional disruption should the current, directional changes continue – which we can be reasonably certain that they will (Settele et al. 2014).

From a botanical perspective, pollination does not seem at risk for now, even though many arctic plants rely heavily on insect pollination (Kevan 1972). More detrimental impacts may arise from the loss of flower resources for late-emerging pollinators as the flowering season continues to shrink (Høye et al. 2013), with potential knock-on effects on both pollinator and plant populations (Miller-Struttmann et al. 2015).

In all ecosystems, the overall service of pollen transport is provided by a variety of insect species and the contributions from different taxa should be weighed together in assessing the net functional change of the target system. In this paper, we have derived such a measure of community-wide plant-pollinator function by weighing species- or group-specific phenologies by their functional importance, and hence arriving at a community-wide functional measure of phenology. Moreover, we have shown how these community-wide phenologies and thus the ecological function vary over time and with environmental drivers (Fig. 1; Supplementary material Appendix 1). As evident from Supplementary material Appendix 1, Fig. A4, taking this approach allows us to identify the disruption of an ecological function at our site, and thus markedly alters our perception of the functional implications of climate change and the resultant phenological changes in the High Arctic. To better detect changes and their functional implications, we encourage researchers

working at other sites and with other systems to translate their records of plant and pollinator communities and their phenologies into such functional measures, and to examine changes therein. Such efforts would significantly increase our understanding of the functional implications of phenological uncoupling at multiple scales.

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Supplementary material (Appendix ECOG-02261 at <www.ecogeography.org/appendix/ecog-02261>). Appendix 1.