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Research Paper

Seasonal release of propagules in mangroves – Assessment of current data

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ABSTRACT

Phenology is often neglected in dispersal research, in spite of its potential effects on the patterns of propagule deposition. Based on peer-reviewed literature, we collated data on propagule release timing for mangroves and aimed at understanding the relation between mangrove propagule release timing and monthly average rainfall and temperature. There were data on 47 species of 25 genera, accounting for 67% of mangrove species, but most (35%) of the available data are related to *Avicennia marina*, *Avicennia germinans* and *Rhizophora mangle*. We found significant correlations ($r > 0.8$, $P < 0.001$) between mangrove propagule release and rainfall, with 72% of data reporting propagule release during the wet season, except in the southernmost latitudes. In the equatorial zone (10°N–10°S), propagules fall from parent trees throughout most of the year with no pronounced production peaks. At latitudes higher than the equatorial zone, propagule release was also significantly correlated with temperature ($r > 0.6$, $P < 0.05$). Our results show phenological complementarity between the northern and southern hemisphere, with a peak in propagule release corresponding to the boreal and austral summer, respectively. We encourage mangrove researchers to report data on propagule release and availability to render an increasingly accurate and precise interpretation of geographic patterns as the current dataset increases, both in terms of geographic and species coverage.

1. Introduction

Over the last years, the phenology of plant species has received increasing attention in ecology (Kramer et al., 2000; Cleland et al., 2007; Körner and Basler, 2010). Most studies have focused on species in temperate zones, where plant phenologies have been correlated with photoperiod and temperature (Huang et al., 2001; Menzel et al., 2005; Vitasse and Basler, 2013), although plant phenologies are very likely controlled by complex interactions among biotic and abiotic factors (Wolkovich et al., 2014). In tropical areas, on the other hand, where photoperiod and temperature show less seasonal variability, phenology was reported to be mainly controlled by precipitation and soil water availability (Singh and Kushwaha, 2005; Couralet et al., 2013). Since anthropogenic activities will increasingly influence these factors, insight into the environmental cues that underlie plant phenology is important for predicting the survival and growth of individuals, the reproductive success of populations and species interactions under shifting climatic conditions (Cleland et al., 2007). Furthermore, phenological data, particularly on the timing of propagule release, are important in dispersal studies, since in combination with temporal variations in the characteristics of the main dispersal vectors, it determines dispersal and deposition patterns (Greene, 2005; Savage et al., 2010; Savage et al., 2012), and hence the potential of individuals to colonize suitable habitats.

In mangrove ecosystems, which have been strongly reduced and fragmented over the last decades due to excessive exploitation and development (Alongi, 2002; Duke et al., 2007; Giri et al., 2011; Mukherjee et al., 2014; Hamilton and Casey, 2016), dispersal is an important determinant of community structure and biogeographic range shifts under changing environmental conditions. Additionally, it can help spread beneficial alleles among populations, fuelling local adaptation (Levine and Murrell, 2003). Hence, there is a strong need for empirical data and models to reconstruct and predict the frequency and the likely trajectories of natural dispersal events (cf. Ngeve et al., 2016) to assess the vulnerability of populations to anthropogenic pressure, extinction, and the likelihood of successful range expansion. However, while the dispersal behaviour of individual mangrove propagules (i.e. dispersal units) and the interaction of the dispersal vectors at play have been studied recently (Van der Stocken et al., 2013; Van der Stocken et al., 2015b), relatively little is known about the temporal dynamics of propagule

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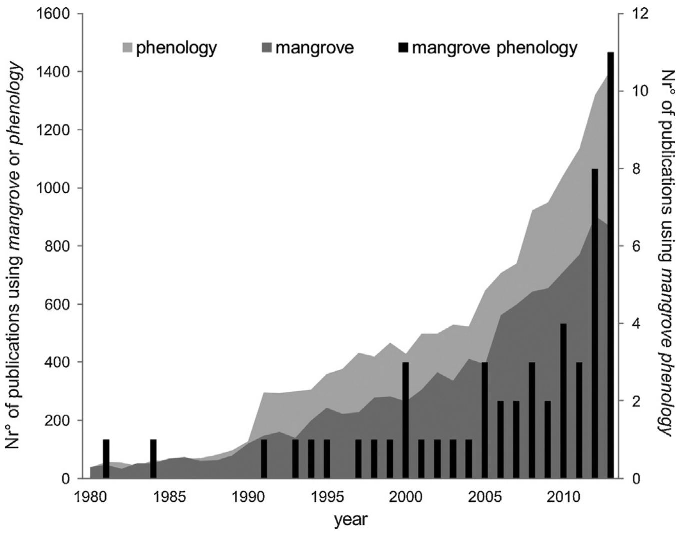

Fig. 1. Number of publications from 1980 through 2013 extracted from the Web of Science™ database with 'phenology' (light grey), 'mangrove' (dark grey), and 'mangrove phenology' (black bars) in the title, keywords or abstract. There is a rapid increase in the number of publications (left y-axis) on phenology and mangroves; but the number of publications on mangrove phenology; though increasing (right y-axis) is still limited.

release and its environmental drivers, hampering the biological realism of model predictions. Such knowledge is important given the temporal variation of dispersal vector properties (magnitude and direction) that may condition the sites of propagule arrival.

Mangrove phenology has received increasing attention (Fig. 1) since these ecosystems represent an important component of primary production in many tropical, subtropical and warm temperate coastal regions (Bouillon et al., 2008). Their role in providing valuable nutrients that support coastal and marine systems has been frequently reported (e.g. Odum and Heald, 1975; Aburto-Oropeza et al., 2008). However, phenological data are mostly restricted to a species and cover time periods that are too short to detect long-term phenological patterns and responses to changes in environmental factors such as rainfall and temperature. Additionally, the drivers mentioned earlier for tropical plant seed phenology (such as soil water availability) are not expected to be merely transposable to mangroves in their waterlogged marine environment. Mangroves present an important research subject for phenology in view of the wide latitudinal range of many species. Therefore, long-term records of mangrove phenology are needed, as well as a quantitative knowledge of their interaction with potential environmental drivers. Here, we assembled most available data on mangrove propagule release timing to assess current knowledge, intending to encourage data gathering on this phenological variable by mangrove researchers worldwide. We recognize that the present dataset on propagule release timing is incomplete, both in terms of species and spatial coverage. However, we do compile data to investigate the presence of latitudinal trends and can explore basic correlations with climatological variables such as monthly average rainfall and temperature. Although correlation does not imply causation, we explore the most straightforward explanations that should be further scrutinized as more data become available.

2. Materials and methods

2.1. Data sources

Peer-reviewed journal articles on mangrove phenology were searched for using the Web of Science™ database. As a keyword, 'phenology' was used and on the outcome of this search, 'mangrove' was used as an additional search operator. The remaining articles were screened for information on the timing of propagule release. Additionally, to ensure that our study includes most of the relevant publications that mention the timing of propagule release, we intensively screened the reference lists of the manuscripts found and searched for missing literature. We continued this procedure until no new data on propagule release was found. We highlight that the list of mangrove plants is a best professional combination of several sources defining which species can be qualified as a 'mangrove', including the original list published by Tomlinson (1986), the World Register of Marine Species (WoRMS) at www.marinespecies.org (Appeltans et al., 2012), as well as selected species published in between (Duke, 2006; Giesen et al., 2007).

We recorded information on the timing of propagule release, the study area, its latitude and longitude, and the season (dry or wet) in which the propagules were released. The information on propagule release was drawn from the text, figures or tables. Data on propagules per se (e.g. dry weight) are not considered in this study because the way in which data were presented often did not allow for such detailed information. We used a binary scale (0–1), marking the months when most propagules were reported (1) and the other months (0). We used the reporting of mature propagules as a proxy for release, when release was not mentioned explicitly. If geographical coordinates were not reported, the study site was located using Google Earth, based on the source publication. Although a special effort was done to retrieve data for West Africa, we found none in peer-reviewed literature.

For correlation with timing of propagule release, data on three environmental variables – monthly average rainfall (MAR), monthly average low temperature (MALT) and monthly average high temperature (MAHT) – were extracted from the World Weather Online database (http://www.worldweatheronline.com). Data on the global distribution of mangroves were taken from the Mangrove Reference Database and Herbarium (Massó i Alemán et al., 2010). To investigate whether global latitudinal patterns in the timing of propagule release exist, monthly binarized data (i.e. presence-absence of propagules) were summed per latitudinal range group (20–37°S, 10–20°S, 10°S–10°N, 10–20°N, 20–28°N) and normalized by dividing by the total number of reported propagule release data per latitudinal range group. The 37°S latitude is 1.45° from the absolute mangrove southern latitudinal range limit (38.45°S, East-Australia); the northern latitudinal limit of mangrove forests is at 32.28°N (Bermuda) (Spalding et al., 2010).

2.2. Data analysis

We calculated the percentage of data per latitudinal range group, the relative abundance of the various mangrove species studies, and the percentage of reported data per country. This allowed us to track knowledge gaps at the level of species and study site.

We computed coefficients and corresponding *P*-values of Pearson correlations between climatological variables and propagule release data (normalized and expressed as a percentage of reports per latitudinal range group), using MATLAB R2014a (MathWorks, Inc.Natick, Mass, USA). We tested for correlation among climatological variables using STATISTICA 8 (Statsoft, Inc., Tulsa, OK, USA). Multiple regression analysis was not considered after we found there was significant multicollinearity among environmental variables.

To illustrate and discuss the importance of phenological data in the study of propagule dispersal and deposition patterns, release locations were plotted for the Indian Ocean area relative to ocean surface current circulation in the Southwest and Northeast monsoon season. Ocean surface circulation patterns were taken from Shankar et al. (2002) and for the Mozambique Channel from Ternon