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Review

Reproducing reproduction: How to simulate mast seeding in forest models

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ABSTRACT

Masting is the highly variable and synchronous production of seeds by plants. Masting can have cascading effects on plant population dynamics and forest properties such as tree growth, carbon stocks, regeneration, nutrient cycling, or future species composition. However, masting has often been missing from forest models. Those few that simulate masting have done so using relatively simple empirical rules, and lack an implementation of process-based mechanisms that control such events. Here we review more than 200 published papers on mechanistic formulations of masting, and summarize how the main processes involved in masting and their related patterns can be incorporated in forest models at different degrees of complexity.

Our review showed that, of all proximate causes of masting, resource acquisition, storage and allocation were the processes studied most often. Hormonal and genetic regulation of bud formation, floral induction, and anthesis were less frequently addressed.

We outline the building blocks of a general process-based model of masting that can be used to improve the oversimplified functions in different types of forest models, and to implement them where missing. A complete implementation of masting in forest models should include functions for resource allocation and depletion, and for pollination, as regulated by both forest structure and weather in the years prior to seed production. When models operate at spatio-temporal scales mismatched with the main masting processes, or if calibration data are not available, simulation can be based on parameterizing masting patterns (variability, synchrony, or frequency). Also, observed masting patterns have the potential to be used as "reality checks" for more process-based forest models wishing to accurately reproduce masting as an emergent phenomenon.

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1. Introduction

Understanding forest ecosystems and predicting their dynamics through models remains an abiding concern of forest researchers. Modeling forest dynamics using only a limited set of fundamental variables represents a challenging task, considering the myriad of components, mechanisms and the degree of complexity involved. Models, however, provide invaluable information to plan sustainable forest management (Monserud, 2003; Taylor et al., 2009). In order to improve the accuracy of forest models operating under changing environmental conditions, ecological processes which have big effects on forest dynamics must be accounted for.

A prominent but overlooked example of such processes is mast-seeding or masting, i.e., the highly variable and synchronous production of seeds by a population of plants. Masting occurs among grass, shrub, and tree species in many different biomes (e.g., Schauber et al., 2002; Abrahamson and Layne, 2003; Poncet et al., 2009; Drobyshev et al., 2010). The synchronized annual variability displayed by masting has been explained by several hypotheses (Sork, 1993; Kelly, 1994; Herrera et al., 1998; Kelly and Sork, 2002). Masting events are thought to be "cued" by particular climatic conditions synchronized over large areas (i.e., Moran effect) in the years that precede flowering (Schauber et al., 2002; Piovesan and Adams, 2001, 2005; Kelly et al., 2013). However, no general consensus has been reached yet on the complete set of processes and mechanisms causing masting (Pearse et al., 2016). Masting is intimately related to other processes of forest dynamics (Fig. 1), such as tree growth (Thomas, 2011; Muller-Haubold et al., 2013; Hacket-Pain et al., 2017), seed dispersal, and regeneration (Vander Wall, 2001; Ascoli et al., 2015). The relative contribution of seed production to annual net primary productivity (NPP) in masting species has been estimated for some species at between 20% and 57% (Mund et al., 2010; Muller-Haubold et al., 2013), and about 15% of stem biomass growth (Mencuccini et al., 1995). The fact that tree growth is reduced in years of heavy seed production (Piovesan and Schirone, 2000) may help to explain the failure of most process-based forest models to reproduce observed inter-annual variability in carbon fluxes or observed biomass growth (Drobyshev et al., 2010; Collalti et al., 2016), as well as the disagreement between modeled growth-climate relationships and observed tree rings (Babst et al., 2013).

Additionally, masting has far-reaching effects on ecosystem functions and services, such as carbon sequestration (Miyazaki, 2013), and on community trophic cascades, including birds and mammals (Ostfeld et al., 1996; McShea, 2000; Clotfelter et al., 2007; Jensen et al., 2012; Zwolak et al., 2016; Selås, 2017) and vectors of human diseases (Ostfeld, 1997; Tersago et al., 2009).

In forestry research, forest models are sets of equations that integrate several mechanisms describing and predicting important forest processes, such as growth, mortality and regeneration (e.g., Monserud, 2003; Vacchiano et al., 2012). Since masting has such widespread influences on forest ecosystem dynamics, implementing it into predictive forest models may contribute to improve their accuracy, not only in terms of modeling seed production but also extending to growth trade-offs, pollen and seed dispersal, establishment success, species migration, cascading trophic interactions, effects of silvicultural treatments, and ecosystem resilience to natural disturbances or climate change. In some of these forest models, seed production has been implemented either as a constant or limitless process, not integrated into allocation (Price et al., 2001), or, more realistically, as a function of NPP or leaf mass (e.g. Bossel, 1996) – however, this is unlikely to fully reproduce the characteristics of masting. Those that did attempt to model masting explicitly used a simplistic implementation, e.g., a regular frequency of years with high seed output (Rammig et al. 2007), neglecting the relationship between masting processes and environmental conditions. Overall, masting has been included in forest models in very few cases (Table 1), be it to look specifically at masting effects, or within large-scale forest ecosystem models in which patterns of seed production have not been specifically developed to incorporate mast seeding.

Inconsistent study design, omitted reporting of effect sizes, and lack of validation of model prediction against observed data mean that no conclusive evidence exists on whether an explicit inclusion of masting in forest models is relevant to accurately predict ecosystem and ecological dynamics. The effect size of including/not including masting in models could possibly vary depending on the desired output variable and on the spatial and temporal span being modeled (e.g., an individual stand vs. a regional forest landscape). Rigorously validated analyses of the accuracy of forest model prediction with and without masting are greatly needed. However, the inclusion of masting in forest models can be crucial on one side for greater realism, and on the other to equip models with a process-based understanding that would enable to produce projections out of the range of their calibration domain, e.g.,

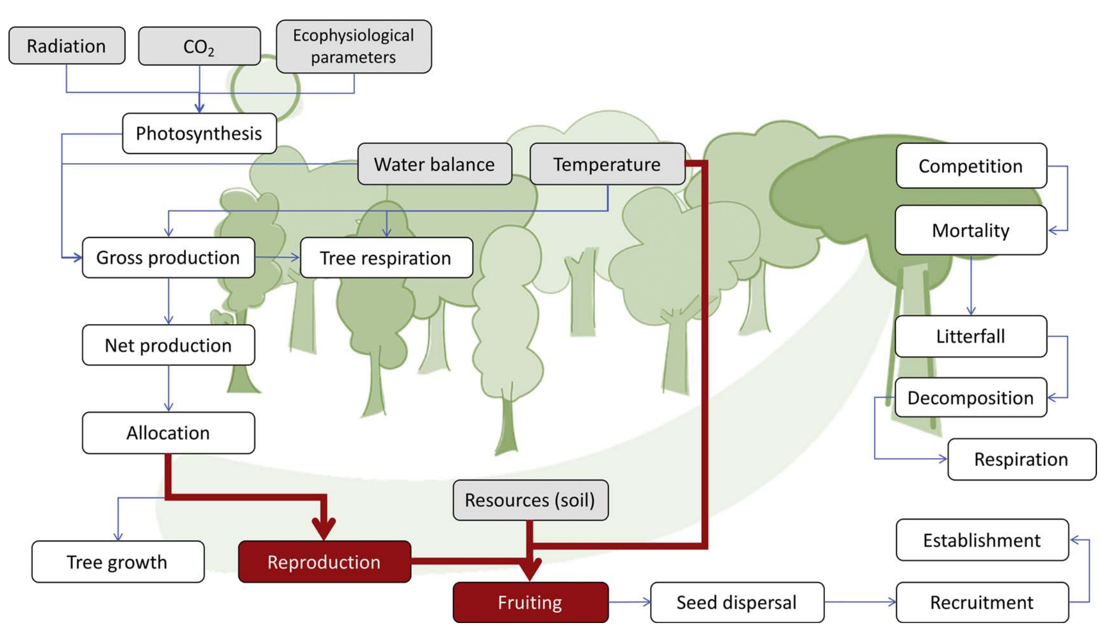

Fig. 1. Simplified process diagram for a generic forest model. Grey boxes: input variables, white: processes, orange (and red arrows): masting-related processes (modified from Fischer et al., 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)