



Original papers

Simulation-based modeling of wild blueberry pollination

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ABSTRACT

The high variability of wild (lowbush) blueberry plants in spatial and genetic structure, in combination with bee foraging behavior varying between species, and the complexity of these factors interacting over time and space, are major obstacles to understanding of pollination dynamics subject to environmental change. The bottom-up modeling paradigm provides an ideal approach to bridging the gap between known mechanisms of individual organisms and unknown spatial–temporal dynamics of pollination at the field scale. By linking empirical data to stochastically-based ecological process modeling, we present a spatially-explicit agent-based simulation model that enables exploration of how various factors, including plant spatial arrangements, outcrossing and self-pollination, bee species compositions and weather conditions, in isolation and combination, affect pollination efficiency throughout a blueberry bloom season. The firmly validated open-source model is a useful tool for hypothesis testing and theory development for wild blueberry pollination researches. Sensitivity analysis suggested that fruit set and resulting measures of productivity such as fruit mass and viable seeds per fruit were sensitive to parameterization of blueberry genotype or clone size and the amount of blueberry plant cover in a field. Fruit set due to pollen compatibility was sensitive to ovule number per flower and foraging bee density. Simulation experiments allowed us to compare bee pollination efficiencies at the bee taxon population level (honey bees, bumble bees, and native solitary bees), the effect of foraging distance from bee nest or colony site on fruit set, and test whether the mechanism of gametophytic self-incompatibility (pre- vs. post-zygotic decision making by the plant) in wild blueberry pollination at the field level matters in estimating yield.

1. Introduction

Wild blueberry (*Vaccinium angustifolium* Aiton) - a unique crop species native to eastern North America, is an economically important fruit crop (Yarborough, 2016). The plant is native to North America (Jones et al., 2014). It is a common understory woody plant of the forest. Farmers clear the forest and then manage the plants for a fruit crop. The plants are not sown and all genotypes are naturally occurring, but managed where they originally colonized. Because of this the crop is often referred to as “Wild Blueberry”. Yield depends heavily on cross-pollination (allogamy) that requires insects, primarily bees (Delaplane and Mayer, 2000; Drummond, 2016; Asare et al., 2017). However, wild blueberry yield is not always a simple linear relationship to bee density (Aras et al., 1996; Yarborough et al., in press Bajcz et al., 2017), it may also be subject to variation of weather and spatial factors. Temperature and rainfall can change blueberry bloom initiation and duration (White et al., 2012) as well as bee foraging activity (Javorek et al., 2002; Drummond, 2016), which makes interactions between the two

organisms too complicated to be predictable in a straight-forward manner. Increasing yield, fruit quality and economic stability in wild blueberry production requires better understanding of the fundamental ecological processes of cross-pollination and how bee species abundance, plant clone (genet) spatial pattern, and weather conditions interact with each other. Although some mechanisms that drive these ecological processes have been studied (Bell et al., 2010; Drummond, 2016), we still lack a holistic understanding of how these dynamic interactions affect pollination efficiency under the influence of changing weather conditions, particularly in a complex context of varying spatial, temporal, taxonomic and genetic scales. Modeling wild blueberry pollination allows us to decipher hidden relationships between organisms to better understand the ecological processes of the wild blueberry cropping system under climate change and to develop improved management strategies for achieving optimal trade-offs between investment and yield (Hanes et al., 2015).

Only a few studies on modeling blueberry pollination have been published, represented by statistical regression models (Eaton and

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Nams, 2012; Kirk and Isaacs, 2012; Yarrow, 2016) and decision support models (Carrière, 2014). In comparison with statistical models that suffer limitations in incorporating the stochastic nature of ecological processes or in presenting environmental heterogeneities (Filatova et al., 2013), the Spatially Explicit Agent-based Modeling (SE-ABM) approach for pollination dynamics offers an alternative lens for understanding the effects of interactions between processes on the individual plant and bee level. Using this approach it is possible to identify interactions within higher-level orders (e.g., pollination efficiency) that emerge (Qu et al., 2013). In past decades, SE-ABMs have been used intensively for pollination modeling, such as predicting bee abundance for specific landscapes (Groff et al., 2016), exploring the effects of pollinator density-dependent preference on pollination (Rands and Whitney, 2010), revealing optimal landscape pattern by examining spatial autocorrelation in honeybee foraging behavior (Henry et al., 2012) and investigating environmental effects on bee movement (Rands, 2014). These successful SE-ABM applications enhanced our confidence that SE-ABM is a valid technical methodology being able to provide novel insights into complex ecosystem dynamics. However, to our best knowledge, we still have not seen SE-ABMs that are able to address specific crop pollination requirements, such as: (1) generating realistic wild blueberry spatial structure; (2) representing plant genetic diversity in terms of pollen compatibility; (3) formulating bee foraging behavior for different taxa, and (4) validating model output against empirical data, which have been considered to be critical to make precise assessments of wild blueberry pollination efficiency.

In this study, we present an SE-ABM that meets the four requirements for wild blueberry pollination research, and describe the modeling logic as well as verification, validation and sensitivity analysis for model assessment. Information regarding model availability, deployment and update is given for user assistance. In addition, we use the model to run three sets of simulations in order to answer the following questions: (1) What are the efficiencies of the three taxa groups of bees (honey bee, bumble bee queens, and native solitary bees) at the population level for pollination of wild blueberry? (2) What is the effect of clone distance to bee nest or colony on expected fruit set and how might this differ with bee taxon? and (3) Does the physiological mechanism of self-incompatibility affect the results of pollination?

2. Methods

2.1. Modeling logic

We modeled wild blueberry pollination in five stages: (1) identified the significant objects or entities and processes (guided by domain experts); (2) represented entities as agents in a spatially-explicit environment; (3) scheduled agents in appropriate temporal scales (guided by domain experts); (4) parameterized agents with empirical data and (5) built the graphic user interface. We used the standard ODD (Overview, Design concepts, and Details, Grimm et al., 2010) protocol to describe the simulation model (Appendix A: Model description).

Entities and processes were defined by identification of relevant organisms and decomposing their interactions into key ecological processes. The model consists of two types of entities: (1) regular entities, e.g., blueberry fields, blueberry clones, stems and flowers and bee pollinators that are visual objects in the real world wild blueberry production system; and (2) virtual entities, marked as gray rectangles, such as the environment, system scheduling, weather and phenology that provide spatial and temporal reference for coordinating the interactions among regular entities (Fig. 1). All entities are organized in a continuous topology in the environment consisting of one or more wild blueberry fields, each of which have a default 2500 m² size or can be user defined (depends on memory availability as well as computational speed of the host computer).

Wild blueberry clones (genetically distinct plants referred to as genets, Bell et al., 2009) and bees are the two primary organisms whose

key ecological processes are represented. We selected four bee taxa “types” as a representation of the bee community associated with Maine wild blueberry agroecosystem (honey bee (*Apis mellifera* L.), bumble bee (*Bombus* sp.), digger bee (*Andrena* sp.), and mason or leafcutting bee (*Osmia* sp.). This is a simplification of the agroecosystem that is characterized by more than 120 bee species, (Bushman and Drummond, 2015). Common bee species that we have field data for that was used in parameterization of this model were *Bombus ternarius* and *B. impatiens* for the bumble bee queens, *Andrena carlini*, *A. vicina*, and *A. Carolina* for the digger bees, and *Osmia atriventris* and *O. inspergens* for the mason bees. The clone processes modeled are vegetative growth (including clone rhizome horizontal spatial expansion) and reproductive growth and phenology (including physiological timing of bloom, production of pollen within flowers on a per stem basis, and acquisition of pollen on floral stigmas, compatible pollen recognition, pollen tube fertilization of ovules, and seed production). The clone dynamics, except pollen tube fertilization of ovules and seed fertilization are clone-specific. The bee processes modeled are taxon-specific and represent: floral search behavior, flower visitation (including pollen extraction and pollen deposition on stigmas) and return to and occupation of nest site (Fig. 2). The interactions between these ecological processes may be spatial, temporal, taxonomic, and genetic or weather relevant, e.g., a flower might accept pollen grains depending on its age (T) and pollen genotype (G); a bee will leave its nest to search for flowers according to the bee species-specific foraging activity (X) subject to weather conditions (W) when the bloom signal (T) has been received. The two organisms are connected via the temporal signaling for the beginning of bloom season, spatial sensing during flower searching and pollen exchange via bee-flower contact.

The entities are modeled as agents interacting with each other in a virtual environment. The environment is represented as continuous space and is referenced with a Cartesian coordinate system. A wild blueberry field is composed of a number of spatially scattered clones. Stems with leaves and flowers attached are randomly distributed within a clone. Bees are spatially initialized by nest site that might be arranged in specific locations in and around a field dependent upon the bee taxa. Bee foraging is modeled as searching and flower visiting from one flower to another that is determined by species-specific flight speed and heading. Pollination, the interaction between plant and bee is defined as pollen exchange at one flower that is located on a specific stem in a specific clone.

The simulation of bloom season covers approximately 30–45 Julian days (a function of growing degree days (GDD)) after the end of the model initialization stage in which all entities are created and arranged. Then all agents are scheduled according to wild blueberry phenology on daily basis for blueberry development, or on minute basis for bee foraging (Fig. 3). Table A1 (supplemental materials) lists all of the entities or agents, their parent entities, the state variable names, and descriptions of the entities. We determined a simulation step is one execution within which a bee can accomplish its activity, i.e. one step for searching or handling flowers in one stem. A different setting for this state variable is used because bee foraging is computationally intensive, particularly in the case of a large abundance of bees or community of bees (multiple taxa) and blueberry clones. When flowers start blooming, bees begin foraging. If a bee can perform one step in 2 min, on average, then it becomes active (completes one cycle) every 2 min (parameter: minutes per step, see parameter Table A2 for detail about taxon specific bee foraging). A cycle per day = 15 h * 30 cycles per hour = 450 cycles per day. We set a period of 8 h for one day considering bee forage between sunrise and sunset, rather than a full day. This is based upon our observations in the field (Drummond, 2016), but in addition, air temperatures in the spring during bloom will generally truncate foraging to less than 8 h per day on most days in May and June. Blueberry clones are scheduled differently, one cycle per day all through the bloom season

To incorporate the stochastic nature of organisms and their

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