



Plant–pollinator population dynamics

Michael A. Fishman, Lilach Hadany*

Department of Molecular Biology and Ecology of Plants, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel

ARTICLE INFO

Article history:

Received 6 March 2010

Available online 22 August 2010

Keywords:

Bees
Bi-stability
Dynamics
Ecology
Individual-level
Mathematical
Model
ODE
Pollination
Population-level

ABSTRACT

We formulate and analyze a multi-generation population dynamics model for pollinators' mutualism with plants. The centerpiece of our model is an analytical expression for population-level plant–pollinator interactions extrapolated from a model of individual-level flowers and bees interactions. We also show that this analytical expression can be productively approximated by the Beddington–DeAngelis formula—a function used to model trophic interactions in mathematical ecology.

© 2010 Elsevier Inc. All rights reserved.

0. Introduction

Flowering plants (angiosperms) are the principal flora in most of the major land habitats. They are a relatively recent group of land plants, originating in early Cretaceous and increasing dramatically in abundance during that period (Crane et al., 1986, 1995). Charles Darwin characterized this sudden appearance of fossil records for a large number of very diverse flowering plant species as an “abominable mystery” (cf. Davies et al., 2004). The current view is that the explosive diversification and present day abundance of angiosperms is due to their co-evolution with animal pollinators, especially insects (Hu et al., 2008).

Despite the subsequent evolution of abiotic-pollination (Crane et al., 1986), the mutualism between flowering plants and their insect pollinators remains an important ecological relationship crucial to the maintenance of both natural and agricultural ecosystems (Kearns et al., 1998). The environmental and economic importance of pollination has been lately emphasized by the reports of the worldwide decline in honeybee and bumblebee numbers (Allen-Wardell et al., 1998; Biesmeijer, 2006). These concerns motivate research aimed at accumulating the knowledge essential to practical plans for ecological restoration involving pollination (cf. Dixon, 2009; Mitchell et al., 2009). This paper is motivated by the hope that mathematical modeling may play a productive role in pollination research (cf. Stout and Goulson, 2002; Lonsdorf et al.,

2009), similar to the one it played in the development of the modern ecosystem theory (Ginzburg et al., 2007; Williams, 2008; Ro-manuk et al., 2009).

Many bees are *central place foragers* (Charnov, 1976; Kacelnik et al., 1986; Olsson et al., 2008). That is, foraging patches where they collect nectar and/or pollen may be several kilometers distant from their nests (cf. Beekman and Ratnieks, 2000; Greenleaf et al., 2007; Pasquet et al., 2008).

In this paper we formulate and analyze a population dynamics model for plants' interactions with central place pollinators. As detailed below, the relevant interactions involve three time scales: (i) handling of individual flowers on the scale of seconds; (ii) foraging bouts/nectar recovery, tens of minutes; and (iii) plants' and pollinators' population densities vary on the scale of years. Thus, this paper is organized as follows.

In Section 1, we exploit the existence of the three distinct time scales in plant–pollinator interactions to derive an analytical expression summarizing individual interactions in population terms.

In Section 2, we show that this expression can be productively approximated by the familiar *Beddington–DeAngelis function* (Beddington, 1975; DeAngelis et al., 1975).

In Section 3, we formulate and analyze a plant–pollinator population dynamics model based on the Beddington–DeAngelis function (see *Appendices* for detailed derivations).

1. Plant–pollinator interactions in population terms

The overall features of the pertinent interactions are summarized in Fig. 1, below.

* Corresponding author.

E-mail addresses: lhadany@post.tau.ac.il, lilach.hadany@gmail.com (L. Hadany).

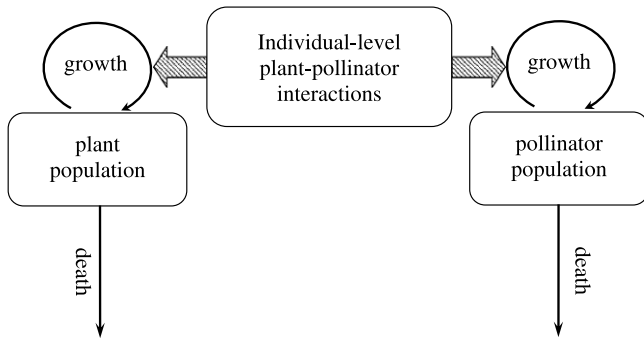


Fig. 1. Pollinators interact with plants promoting cross-pollination that contributes to plant population renewal. Pollinators gather food (e.g. nectar and pollen). Some of the food is used for “maintenance”, and the rest is used to provision offspring assuring pollinators’ population renewal.

We start by considering the dynamics of individual-level interactions between bees and flowers wherein they forage. As discussed above, bees may collect food at a distance of several kilometers from their nests. Hence, a foraging bout’s duration: travel from the nest to a foraging patch, food collection, flight back to the nest, and unloading; may constitute a major portion of an hour (Westphal et al., 2006). However, handling of the individual flower is a matter of seconds (cf. Stephanou et al., 2000; Jones and Reithel, 2001). Moreover, the time spent in foraging patches may be considerably less than half the total foraging time (Schmid-Hempel and Schmid-Hempel, 1987).

To estimate the effects of an individual pollinator’s visit on a nectar bearing flower, we reason as follows. It is known that flowers produce nectar continuously (Castellanos et al., 2002; Hernandez-Conrique et al., 2007; Keasar et al., 2008). Furthermore, nectar production appears to be subject to feedback inhibition i.e., nectar removal stimulates replenishment (Castellanos et al., 2002). On the other hand, we know that bees leave scent marks on flowers, and use these marks to reject recently depleted flowers (cf. Stout and Goulson, 2002; Saleh et al., 2006). Hence, the model must incorporate a period of recovery after a pollinator’s visit.

Reports on the time course of bees’ rejection of marked flowers vary extensively: from a half-life of less than a minute (cf. Williams, 1998) to a half-life of several hours (cf. Yokoi and Fujisaki, 2009; Fig. 3b). This variation has been attributed to the identities of the participating pollinators (cf. Yokoi et al., 2007), the differences in nectar recovery rates among plants (Stout and Goulson, 2001; 2002), and the fact that pollinators can learn from experience (Saleh and Chittka, 2006). Stout and Goulson (2001, 2002) estimated the average delay in acceptance of marked flowers to be 20–40 min. The last result is supported by direct measurements of nectar recovery rates (cf. Gilbert et al., 2001). That is, time scale of the recovery process is comparable to the time scale of pollinators’ foraging bouts.

Given the relatively long recovery times, we have to divide the flowers in a foraging patch into four subclasses: occupied (by a pollinator) vs. unoccupied; and marked (by pollinator’s footprints) vs. unmarked.

- Let the density of unmarked and unoccupied flowers be denoted by U , and let the density of marked and unoccupied flowers be E . We denote the rate coefficient for nectar recovery/fading of marks by k_r (see Table 1 for a summary of key model variables).
- We denote the density of free pollinators (as opposed to ones occupying a flower) within that patch by V , and the corresponding value for foragers outside the patch (i.e. pollinators in transit between the nest and the patch, or unloading in the nest) by W . We assume that pollinators arrive in the patch at rate $k_a W$ and depart at rate $k_d V$.

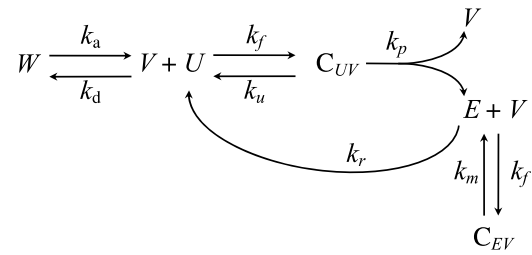


Fig. 2. A “kinetic” scheme of plant–pollinator interactions summarizing the discussion above.

- We assume that the rate at which pollinators in the patch visit flowers is proportional to the product of their respective densities. Since bees cannot distinguish between marked and unmarked flowers except via a close approach (Williams, 1998), we define the same rate coefficient, k_f , for pollinator visits to marked and unmarked flowers. Finally, we denote the respective densities of the two types of pollinator-occupied flowers by C_{UV} and C_{EV} .
- Even without a recent depletion by a pollinator, flowers exhibit great intra-specific variation in the rewards they offer. i.e., at any given time, a non-negligible proportion of unmarked flowers contain little or no reward. (cf. Zimmerman, 1988; Goulson et al., 2007). That is, a visiting bee may depart an unmarked flower without collecting any reward—we denote the pertinent rate constant by k_u . We denote the rate constant for productive interaction by k_p . Finally, we denote the rate constant for pollinators rejecting a marked flower by k_m .

The pertinent features of individual-level interactions are summarized in Fig. 2.

Both the quantity of food collected—and hence survival and recruitment of new pollinator cohorts—and the degree of cross-fertilization achieved by plants are proportional to the extent of productive plant–pollinator interactions. Thus, to formulate a population-level model for plant–pollinator interactions, we must derive a formula expressing C_{UV} as a function of plant and pollinator total population densities: x and y respectively.

To achieve this purpose, we take advantage of the three distinct time scales involved in plant–pollinator interactions, namely:

- Plant and pollinator population densities vary on the scale of their respective life-spans — several months or more for most species of plants and central-place foragers.
- The duration of a foraging bout is of an order of an hour.
- Finally, a bee’s visit to an individual flower is a matter of seconds.

Hence, we can take advantage of the analytical method of separation of time scales (cf. Segel and Slemrod, 1989; Borghans et al., 1996). In this approach, fast processes are assumed to reach steady state (provided it is feasible) while the slower processes unfold —quasi steady-state approximation (QSSA).

In Appendix A we show that, on the time scale of plant and pollinators’ population dynamics, we have the following expression for C_{UV} as a function of x and y .

$$\Phi(x, y) \equiv C_{UV}(x, y) = \frac{2\alpha xy}{\sqrt{\sigma(x, y)} + \rho(x, y)}$$

where

$$\rho(x, y) = 1 + \alpha x + \alpha \beta y \tag{1.1a}$$

and

$$\sigma(x, y) = \rho(x, y)^2 - 4(1 - s)\alpha^2 \beta xy.$$

The parameters α , β , and s represent the functional relations among the parameters in Fig. 2 which are obtained under the QSSA. Namely,

Download English Version:

<https://daneshyari.com/en/article/4502708>

Download Persian Version:

<https://daneshyari.com/article/4502708>

[Daneshyari.com](https://daneshyari.com)