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Ecological and evolutionary consequences of spatial and temporal variation in pre-dispersal seed predation

Annette Kolb*, Johan Ehrlén, Ove Eriksson

Department of Botany, Stockholm University, SE-10691 Stockholm, Sweden

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Abstract

Pre-dispersal seed predation may have important effects on population dynamics and trait evolution in plants. In this review, we first present a conceptual framework of the strength of pre-dispersal seed predation and its variation in space and time. We consider the interaction between plants and their seed predators to be "strong" when it affects plant population dynamics or causes changes in plant trait–fitness relationships, and "weak" when it has no such effects, and propose ways of how to adequately assess these effects. Second, we review the ecological literature between 1991 and 2005 to evaluate documented effects of pre-dispersal seed predation on plants and draw five major conclusions. (1) Pre-dispersal seed predation rates are usually low but sometimes high, and show a considerable variation in space and time. (2) Direct evidence suggests that pre-dispersal seed predation can have a significant effect on recruitment and plant population growth rate. Accumulating evidence of seed-limited recruitment suggests that such effects are common. (3) Pre-dispersal seed predation affects selection on several plant traits, such as flowering phenology and flower number, which are usually interpreted mainly in the context of plant–pollinator interactions. (4) The patterns of variation in the interactions between plants and pre-dispersal seed predators suggest that geographic selection mosaics may be common. (5) Although there are numerous studies estimating seed predation, there are still rather few studies that have aimed at examining the interaction explicitly in terms of effects on plant population dynamics and trait selection. From these we know that seed predators can have important, and often variable, effects on plant population dynamics and trait evolution. However, it still remains to assess how important they are across study systems and relative to other aspects of the plant's biotic and abiotic environment.

Keywords: Interaction strength; Plant–animal interactions; Plant population dynamics; Plant population growth rate; Plant trait evolution; Plant trait–fitness relationships

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Introduction

Plants interact with a multitude of mutualistic and antagonistic animals. Mutualistic interactions can be important for pollination and seed dispersal, while antagonistic animals may cause damage to plants by removing plant parts or by feeding on their seeds. Among the antagonistic animals, herbivores commonly

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*Corresponding author. Present address: Vegetation Ecology and Conservation Biology, Department of Ecology and Evolutionary Biology, FB2, University of Bremen, Leobener Str., D-28359 Bremen, Germany. Tel.: +49 421 218 7087; fax: +49 421 218 7052.

E-mail address: akolb@uni-bremen.de (A. Kolb).

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eat only parts of a plant, leaving the remainder to regenerate, while seed predators actually kill individual plants. Harper (1977, p. 457) noted that "a great many studies have been made of the magnitude of predation" but that "very little help to determine whether predation is relevant either to the evolution or the population biology of plants". For long, a common belief was that plants have more impact on the population dynamics of their insect herbivores than herbivores have on plant population dynamics (Crawley, 1989). A growing number of studies, however, provide evidence for seed predators to influence the abundance, distribution or dynamics of plant populations (Louda, 1982; Louda and Potvin, 1995; Maron et al., 2002; Fröborg and Eriksson, 2003; Rose et al., 2005; reviewed by Maron and Crone, 2006), and many emphasize their selective force and role in the evolution of traits (Brody, 1992; Cariveau et al., 2004; Whitney and Stanton, 2004; Kon et al., 2005; Rose et al., 2005). Correspondingly, seed predation has been suggested to play a crucial role in plant population dynamics and to act as a strong selective force in the evolution of traits (Hulme and Benkman, 2002).

Nonetheless, our ability to adequately predict the ecological and evolutionary consequences of seed predation is still limited. While many of the studies on seed predation effects on plants are snapshots in space and time, it is also well known that changes in seed abundance (Nilsson and Wästljung, 1987; McKone et al., 1998) or seed predator densities (Honek and Martinkova, 2005) as well as the presence of other interacting species (Strauss and Irwin, 2004) and higher trophic levels (von Zeipel et al., 2006) may cause seed predation rates to vary spatially and temporally (e.g. Crawley, 1992). Explicit knowledge of such spatial and temporal variation in the magnitude and effects of seed predation may be crucial to our ability to predict plant population dynamics or evolutionary trajectories. For example, if a seed predator consistently shifts plant population growth from increasing to decreasing in one type of habitat but not in another, then the plant will be less frequent or even absent in the first and more common in the second habitat. On the other hand, if the seed predator substantially reduces plant population growth only in some years and in varying sites, its longer-term effect on the distribution pattern of the plant may be more diffuse. Thus, interactions with seed predators may be an essential component of the regional dynamics (or metapopulation dynamics; Hanski 1999) of plant populations. Similarly, if seed predation rates are consistently related to certain plant traits (e.g. flowering phenology, flower number or seed size) over time and spatially variable, this may create coevolutionary hotspots (Thompson, 2005). If there is temporal variation in plant trait–fitness relationships resulting in a continually shifting mosaic of plant–seed predator interactions, then there will be weak evolutionary effects of seed predation. Accordingly, the spatial and temporal patterns of seed predation are relevant in two different theoretical contexts, metapopulation theory (Hanski, 1999) and the theory of geographic mosaics of coevolution (Thompson, 1994, 2005). To assess to what extent plant–seed predator interactions are important for metapopulation dynamics and coevolutionary mosaics, respectively, we need a firm basis of knowledge of the spatial and temporal patterns of seed predation effects on population dynamics, and of how seed predation influences plant trait–fitness relationships.

In this paper, our objective is to examine how spatial and temporal variation in the intensity and outcome of pre-dispersal seed predation influence plant population dynamics and plant trait evolution. Pre-dispersal seed predation takes place while seeds are still on the mother plant, in contrast to post-dispersal seed predation which occurs once seeds have dispersed away from their parent. Species involved in pre-dispersal seed predation tend to be small and specialized, the large majority belonging to the insect orders Coleoptera, Diptera, Hymenoptera and Lepidoptera (Hulme and Benkman, 2002). For better comparability of effects, we focused on insects, excluding other groups of predators such as granivorous birds. First, we present a conceptual framework of seed predation interaction strength and its variation in space and time. We consider the interaction to be "strong" when it affects the population dynamics of a species or causes changes in plant trait–fitness relationships, and "weak" when it has no such effects, and propose ways of how to adequately assess these effects. Even though we concentrate on pre-dispersal seed predation, this framework is also applicable to other plant–animal interactions such as other forms of herbivory or pollination as well as to species interactions in general. Second, we review the ecological literature between 1991 and 2005 (i) to investigate how researchers have generally assessed the effects of pre-dispersal seed predation on plants, (ii) to review the evidence of pre-dispersal seed predation being a "strong" interaction given our definition above, (iii) to explore how strong and how variable pre-dispersal seed predation is in space and time and which consequences this may have for the ecology and evolution of plants and (iv) to test for potential differences among different plant life histories and habitat types.

The meaning of "strong interactions"

Many theoretical concepts and empirical approaches have been used to describe and measure the strength of interactions among species, with the different meanings of "interaction strength" depending on the context in which they are used (for recent reviews see e.g. Laska and Wootton, 1998; Berlow et al., 1999, 2004; Wootton