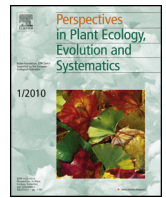




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## Review

# On the evolutionary and ecological value of breaking physical dormancy by endozoochory



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## ABSTRACT

Seed dispersal by animal vectors (endozoochory) is ubiquitous, significantly shaping plant communities. Plants that produce seeds with physical dormancy (PY), including many agriculturally and economically important species, constrain the timing of seed germination via impermeable seed coats. PY seeds consumed by animals often receive the dual benefit of dormancy-breaking during passage through the animals' gut and dispersal outside the parent plant community. In this review we synthesized the current endozoochory literature, paying particular attention to germination ecology and seedling establishment in PY species, before suggesting future research based on critical gaps in current knowledge. To fully synthesize available data, we created a database of 139 PY seed-herbivore pairs from studies focused on dormancy-breaking during gut passage and germination success after defecation. Overall, we draw four main conclusions: (1) the type of herbivores consuming PY species determine the total number of seeds germinating following gut passage; (2) an impermeable seed coat likely protects the internal structures of seeds during chewing and gut passage, however traits previously considered important prerequisites for seed survival during gut passage, such as small seed size (<3 mg) and spherical shape, need to be reassessed; (3) PY does not always break during gut passage and seeds may utilize alternative dormancy-breaking cues in the post-dispersal environment, e.g. seasonal temperatures or secondary dispersal; (4) dormancy-breaking of PY seeds by herbivore ingestion is likely an exaptation, i.e. a trait that performs a function for which it did not originally evolve. However, PY seeds benefit significantly from herbivore dispersal outside the parent community and gut passage may free seeds from risk of predation by insects. We suggest future studies deviate from commonly investigated plant families (e.g. Fabaceae) and incorporate the post-dispersal germination environment to fully elucidate the mechanisms of germination and seedling establishment in PY species.

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## 1. Introduction

Seed-producing plants maximize offspring survival by investing heavily in seed traits. Physical dormancy (PY), where the germination of viable seeds is constrained under otherwise favorable conditions, occurs due to the seeds palisade layers of lignified Malpighian cells becoming impermeable during maturation drying (Baskin and Baskin, 2004; Long et al., 2014; Willis et al., 2014). PY has been described for ~25% of known plant species from 18 angiosperm families (Baskin and Baskin, 2014; Baskin et al., 2000). After dispersal, seeds with PY will persist in the soil until biotic or abiotic factors make them permeable to water (Baskin and Baskin, 2014; Jaganathan and Liu, 2014b; Long et al., 2014; Van Assche et al., 2003). When the embryo of PY species does not have any physiological dormancy (PD), i.e. with combinational dormancy (PD + PY) (sensu Baskin and Baskin, 2004), these seeds readily germinate after becoming permeable to water, provided suitable conditions for germination exist (Baskin and Baskin, 2014).

Abiotic cues such as high summer soil temperatures in the tropics, and winter freeze-thaw cycles in the arctic, often break PY and synchronize seed germination with the growing season (Quinlivan, 1968; Taylor, 2005; Van Assche et al., 2003; Baskin and Baskin, 2014). Some seeds may require specific events, such as fire, to break PY, although the erratic nature of fire and associated mortality risks to embryos make this theory controversial (Jaganathan, 2015). Alternatively, biotic factors such as passing through the gut of animals can successfully break PY (Rolston, 1978). However, the underlying ecological and evolutionary mechanisms responsible for breaking PY remain unresolved.

The ingestion and dispersal of seeds by animal vectors is broadly defined as endozoochory (Fenner and Thompson, 2005; Traveset et al., 2007; Van der Pijl, 1982) and has been a central focus in seed research for several decades (Janzen, 1971; Ridley, 1930). Frugivorous vertebrates such as mammals, birds and reptiles commonly disperse seeds via defecation after fleshy fruits are consumed (Howe, 1986; Pakeman et al., 2002; Ridley, 1930; Samuels and Levey, 2005). Approximately 27% of angiosperm and 64% of gymnosperm lineages have evolved fruits to attract animal dispersers (Traveset et al., 2007). Animal vectors often deposit seeds away from parent plant communities, aiding in plant colonization of new locations and reducing resource competition with parent plants during seedling establishment, (Howe and Smallwood, 1982; Traveset et al., 2007).

Previous reviews have focused on either the role of endozoochory in seed germination (see Traveset et al., 2007) or on how seed germination is controlled by dormancy (see Finch-Savage and Leubner-Metzger, 2006), but there is no review on the germination ecology of PY seeds that experience endozoochory. In general, studies addressing endozoochory of PY seeds focus only on the effect that passage through an animal gut has on germination. Yet the fate of defecated seeds is also affected by various seed- and herbivore-dependent factors that need to be considered. PY is present in many agriculturally and economically important species, and endozoochory has received particular attention from invasion ecologists investigating the spread of alien species. Currently, our knowledge of germination ecology in endozoochorously dispersed seeds and the factors influencing PY loss during gut passage remain disjointed.

In this review, we aim to synthesize the existing literature on the germination ecology of endozoochorously dispersed PY seeds and highlight critical gaps in current knowledge. We performed a literature search in the ISI web of knowledge and JSTOR using the key terms ‘hard seed coats and endozoochory’ and/or ‘physical dormancy and endozoochory’ to identify studies that have investigated the effects of endozoochory on PY species. Manuscripts were screened and verified for the inclusion of PY seed species. Specifically, we extracted studies in which authors had collected PY seeds from pats after seeds had been eaten by herbivores in the field (“pats” in Table A.1 in the Supplementary material), or in which seeds had been experimentally fed to herbivores and seeds had been collected from fresh pats (“fed” in Table A.1 in the Supplementary material). We excluded studies where seeds were simply treated with rumen contents unless there was evidence to support the consumption of these seed species by herbivores (e.g. Venier et al., 2012; Yu et al., 2012) (“rumen” in Table A.1 in the Supplementary material). Studies were included only if they evaluated dormancy loss or germination ability of seeds after egestion. Studies focusing on the effect of gut passage on other forms of dormancy and/or non-dormancy (e.g. Cáceres and Monteiro-Filho, 2007; Traveset, 1998) were excluded from our review. We also excluded species and/or studies where authors noted that the species possessed a hard seed coat, but evidence for water-impermeable seed coat in that species does not exist (e.g. *Phillyrea angustifolia* in Grande et al., 2013; Yamashiro and Yamashiro, 2006). For the purpose of this review, we use the term ‘herbivore’ to group all vertebrates that consume and defecate seeds.

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