## Arboreal squirrels and the oaks: The global biogeography of a plant-animal mutualism

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The process of seed and nut dispersal by scatter hoarding animals is a complex interaction between plant species and the animals that act as both seed predators and agents of seed dispersal. Given the community of species (insects and vertebrates) that often collectively influence the seed predation and dispersal process, it is reasonable to conclude that, in many cases, these relationships result from a weaker, diffuse mutualism between the seed dispersers and the seed plant(s) on which they feed. However, in this study, we provide evidence from several independent lines of investigation that the relationship between multiple genera of arboreal squirrels and the oaks reflect a strong direct mutualism.

Our studies are based on extensive analyses of acorn characteristics, behavioral responses of squirrels to these characteristics, several germination studies in which we simulated squirrel pruning and damage to acorns of multiple oaks species followed by acorn germination and establishment success, and a series of recent behavioral field experiments that demonstrate how some squirrels manage acorn scatter hoards and control pilferage by conspecific competitors.

Collectively these studies show that (1) specific characteristics (e.g., acorn shape, chemical gradients, germination schedules) collectively influence the dispersal process by squirrels, (2) arboreal squirrels, unlike other mammalian and avian acorn consumers, exhibit strong innate behavioral responses to some of these characteristics, (3) numerous acorn species in North America and Asia exhibit specific, but contrasting, germination morphologies which enable young seedlings to escape several stages of predation by arboreal squirrels, and (4) specific behavioral decisions by arboreal squirrels when scatter hoarding acorns significantly increase the probability of oak dispersal. Results of these studies suggest that several genera of arboreal squirrels may have a disproportionate impact on oak regeneration in a number of systems. We argue that future conservation efforts should focus on the keystone role that arboreal squirrels may play in forest regeneration.