



Quantifying the outcome of plant–granivore interactions

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In many interspecific interactions, the balance of costs and benefits varies with ecological circumstances. As a prominent example, seed-caching granivores may act as seed predators and reduce plant recruitment or as seed dispersers and increase recruitment, making it difficult to interpret whether differences in seed removal by granivores would harm or benefit plant populations. We used a heuristic model to evaluate the outcome of plant–granivore interactions, using commonly measured field data: probability of seedling emergence when granivores are excluded, and emergence of cached and uneaten seeds. Published studies to date suggest that the outcome of plant–rodent interactions tends weakly towards mutualism, but differs among particular plant–granivore pairs and ecological conditions, supporting the notion of context-dependence. A modeling framework also allowed us to distinguish parameters that affect the qualitative outcome of plant–granivore interactions from those that do not. Similar approaches would facilitate more efficient and cost-effective evaluation of complex species interactions.

Many interspecific interactions involve both costs and benefits, and the balance of these determines where the net outcome falls between mutualism and antagonism (Bronstein 1994, Schupp et al. 2010). The interaction between plants and scatterhoarding vertebrates is a particularly interesting example of this continuum. Granivorous animals play a dual role in plant regeneration. On one hand, such animals often consume large quantities of seeds, which should reduce recruitment. On the other, they also store considerable amounts of seeds and some of the cached seeds may remain uneaten because animals forget caches, store more seeds than they are capable of eating, or die before consuming stored seeds (Jansen and Forget 2001). Cached seeds often have higher probabilities of germination and establishment than seeds that were not removed because scatterhoarding may reduce the risk of desiccation, consumption by strict seed predators, and density-dependent mortality near parent plants (Vander Wall 2001, Hulme and Kollmann 2005). In addition, seeds are sometimes transported to microsites where seed and seedling survival are relatively high (i.e. directed dispersal: Briggs et al. 2009).

It is often unclear if granivores aid plant recruitment or if the costs of seed predation outweigh the benefits of caching. Many studies focus solely on the magnitude of seed removal and assume that the removal agents act mostly as antagonists (seed consumers) or mutualists (seed dispersers). Thus, interpretation of particular experiments can be contentious (Gómez et al. 2003 vs den Ouden et al. 2005, Vander Wall et al. 2005). In principle, one could conduct large-scale control-exclusion experiments to directly measure the net consequences of seed-caching for plants, but this is

logistically challenging. Alternatively, one could quantify the individual components of plant–granivore interactions, such as the proportion of seeds removed, consumption rates, relative germination rates, etc. and combine them algebraically to determine the net outcome (Schupp et al. 2010). However, even though there are several methods that enable tracking seeds removed by granivores (reviewed by Forget and Wenny 2005), it is seldom feasible to measure all components of plant–granivore interactions. Therefore, evaluating the costs and benefits of seed caching remains the most important method of gauging if the interaction between seed caching granivores and plants is mutualistic or antagonistic (Jansen and Forget 2001, den Ouden et al. 2005, Theimer 2005).

Here, we elaborate on past attempts to quantify the outcome of plant–granivore interactions by providing a heuristic model of antagonistic or mutualistic relationships that enables evaluating the net outcome of plant–granivore interactions, using two variables that are among the most commonly measured: emergence rates of seeds that are cached, and emergence rates of seeds that are not handled by granivores. We use data from several published studies of rodent granivory to assess whether plant–granivore interactions tend to be beneficial versus detrimental to plant populations across these studies. Importantly, this approach explicitly identifies some processes that do not need to be measured to determine the qualitative outcome (mutualism vs antagonism), even though they affect the magnitude of costs or benefits.

In addition to evaluating the specific case of plant–granivore interactions, our approach is generally relevant in that the net outcome of interspecific interactions is increasingly

recognized as context-dependent (Holland and Bronstein 2008). In some cases, the net outcome is relatively consistent, even if occasional exceptions exist; for example, Chamberlain and Holland (2009) reviewed ant–plant mutualisms and showed that the outcome is beneficial on average, even though exceptions to this rule were some of the first examples that inspired Bronstein’s (1994) now-classic review. In others, the net outcome may depend highly on population sizes of one or both players, environmental conditions, or presence of other interacting species. Identifying how species interactions change in time and space has been identified as a major challenge in ecology (Agrawal et al. 2007), and yet we lack efficient and cost-effective methods to measure the outcome of species interactions.

A model of plant–granivore interaction

Whether scatterhoarding granivores are beneficial or detrimental for plant populations depends on whether recruitment with seed-caching granivores is greater or less than recruitment without seed caching (Jansen and Forget 2001). In other words, predation is beneficial when:

$$\left[\begin{array}{c} \text{seedling} \\ \text{emergence} \\ \text{without granivores} \end{array} \right] < \left[\begin{array}{c} \text{seedling} \\ \text{emergence} \\ \text{with granivores} \end{array} \right] \quad (1)$$

In and of itself, this inequality eliminates some of the complexity of assessing the outcome of plant–granivore interactions. In principle, the net effect of granivores on plant populations would be determined by the change in seedling emergence, multiplied by the importance of seedling emergence for plant population dynamics, e.g. the sensitivity of population growth rate to changes in emergence (cf. Maron and Crone 2006, Schupp et al. 2010). However, since both sides of the inequality above would be multiplied by this term, it would drop out of Eq. 1. In other words, although the magnitude of costs or benefits depends on post-emergence parameters, the qualitative outcome would not, unless caching also affected demographic parameters following seedling emergence. Such effects have rarely been documented, though some examples exist (Vander Wall 1993).

In order to relate this relationship to data we, first, defined a rate of emergence, without granivores, from the ground surface, e_S . This rate can be estimated directly from the rate of seedling emergence in consumer exclusion cages (widely used in plant–granivore research, Maron and Simms 1997, Orrock et al. 2008, Goheen et al. 2010, Zwolak et al. 2010):

$$e_S < \left[\begin{array}{c} \text{seedling} \\ \text{emergence} \\ \text{with granivores} \end{array} \right] \quad (2)$$

In the presence of granivores, a certain fraction of seeds, p_H , is harvested (removed or eaten in situ). Of the removed seeds, most are consumed, but a fraction is cached and never recovered. We refer to this fraction as p_C . Finally, of cached seeds, some proportion eventually germinates and emerges as seedlings. We call this proportion e_C . We can use these

constants to represent seedling emergence with seed-caching granivores, on the right-hand side of the equation:

$$e_S < p_H p_C e_C + (1 - p_H) e_S \quad (3)$$

(i.e. the proportion of seeds that are taken multiplied by the probability they emerge from caches, plus the proportion that are not taken, multiplied by emergence of seedlings on the soil.)

The variable p_H is commonly measured directly, in field (Vander Wall 1992, 1993, 2002, Gómez et al. 2008). Alternatively, p_H might be estimated from the ratio of seedlings emerging in consumer exclusion cages with openings, $(1 - p_H) e_S$ to seedlings emerging in consumer exclusion cages, e_S :

$$p_H = 1 - \frac{(1 - p_H) e_S}{e_S} \quad (4)$$

Note that using emergence from cages to estimate removal by granivores assumes cages do not affect background germination rates, e.g. it assumes cages do not affect the proportion of seeds that remain dormant in the soil. It is also useful primarily for plant species that have high emergence during the first few years, rather than long-lived seed banks.

Of the two remaining parameters, e_C may be estimated by finding caches and documenting germination or by measuring emergence from artificial seed caches (Table 1). However, p_C , the proportion of seeds cached and left uneaten, is often not feasible to measure (Table 1): it is very difficult to find the caches in the first place, and it is also difficult to track seeds that have been recached, i.e. cached and retrieved or pilfered and then cached again elsewhere (Vander Wall and Joyner 1998). Therefore, we rearranged the inequality above to find out what values of p_C would be necessary for granivores to be beneficial:

$$\begin{aligned} e_S &< p_H p_C e_C + (1 - p_H) e_S \\ &\downarrow \\ e_S - (1 - p_H) e_S &< p_H p_C e_C \\ &\downarrow \\ (1 - 1 + p_H) e_S &< p_H p_C e_C \\ &\downarrow \\ e_S p_H &< p_H p_C e_C \\ &\downarrow \\ \frac{e_S p_H}{p_H e_C} &< p_C \\ &\downarrow \\ \frac{e_S}{e_C} &< p_C \end{aligned} \quad (5)$$

This inequality means that whether granivores are beneficial depends on whether the proportion of cached seeds that are uneaten is greater than the ratio of establishment on bare soil to establishment from caches. For convenience, we will

Table 1. Experiments on seedlings emergence from seeds that were scatterhoarded by birds or rodents vs emergence from seeds left on the surface. Parameter \hat{p}_c , the ratio of emergence probabilities of seeds from artificial caches to seeds left on surface, denotes the minimum proportion of seeds that would have to be cached and uneaten for granivores to benefit plant recruitment.

Study	Seed species	Potential scatterhoarding species*	e_s	e_c	\hat{p}_c	Comments
Jensen 1985	<i>Fagus sylvatica</i>	<i>Apodemus flavicollis</i> , <i>Myodes glareolus</i>	0	0.167	0	seeds scattered on top of the litter layer did not germinate; seeds buried at 3 cm germinated in two out of three vegetation communities
Sork 1985	<i>Gustavia superba</i>	<i>Dasyproctasp.</i>	0.744	0.866	0.860	seeds buried 1–2 cm into soil vs placed on top of the soil
Vander Wall 1992	<i>Pinus jeffreyi</i>	<i>Tamias amoenus</i>	0.009	0.552	0.016	seeds buried 1 cm into soil vs left on the soil or litter surface
Vander Wall 1993	<i>Purshia tridentata</i>	<i>Tamias amoenus</i>	0.022 (0.008**)	0.407 (0.190**)	0.054 (0.043**)	seeds buried 1 cm*** into soil vs left on the surface
Kollmann and Schill 1996	<i>Corylus avellana</i>	<i>Apodemus flavicollis</i> , <i>A. sylvaticus</i> , <i>Myodes glareolus</i> , <i>Garrulus glandarius</i>	0.055	0.495	0.111	seeds buried 5–6 cm into soil vs left on the surface
Kollmann and Schill 1996	<i>Quercus petraea</i>	<i>Apodemus flavicollis</i> , <i>A. sylvaticus</i> , <i>Myodes glareolus</i> , <i>Garrulus glandarius</i>	0.146	0.898	0.163	seeds buried 5–6 cm into soil vs left on the surface
Asquith et al. 1999	<i>Hymenaea courbaril</i>	<i>Dasyprocta</i> spp.	0	0.214	0	seed pods buried flush with the soil surface vs left on the surface; only buried ones germinated
Garcia et al. 2002	<i>Quercus rubra</i>	<i>Tamiasciurus hudsonicus</i> , <i>Cyanocitta cristata</i>	0.066	0.557	0.119	seeds buried 1 cm into soil vs left on the surface
Borchert et al. 2003	<i>Pinus coulteri</i>	Mostly <i>Dipodomys agilis</i> , but also <i>Chaetodipus californicus</i> and <i>Peromyscus maniculatus</i>	0.473	0.634	0.747	study conducted in a burned forest; seeds buried 1 cm into soil vs left on the surface
Tomback et al. 2005	<i>Pinus flexilis</i>	<i>Peromyscus maniculatus</i> , <i>Dipodomys ordii</i>	0.114	0.502	0.226	seeds buried 2 cm into soil or in vegetation tussock vs left on the surface
Borchert 2006	<i>Marah macrocarpus</i>	<i>Peromyscus</i> spp.	0	0.583	0	only buried seeds (depths 2–16 cm) germinated
Briggs et al. 2009	<i>Pinus jeffreyi</i>	<i>Peromyscus maniculatus</i> , <i>Tamias amoenus</i> , <i>Tamias quadrimaculatus</i> , <i>Spermophilus lateralis</i>	0.047	0.306	0.154	seeds buried 5 or 25 mm into soil vs left on the surface
Keyes et al. 2009	<i>Pinus ponderosa</i>	<i>Tamias amoenus</i> , <i>Spermophilus lateralis</i>	0.07 (0.01**)	0.45 (0.08**)	0.156 (0.125**)	seeds buried 1 cm into soil vs left on the surface
Beck and Vander Wall 2010	<i>Prunus andersonii</i>	<i>Ammospermophilus leucurus</i> , <i>Peromyscus maniculatus</i> , <i>Perognathus parvus</i> , <i>Dipodomys panamintinus</i>	0.008	0.32	0.024	seeds buried 1–5 cm into soil vs left on the surface
Klinger and Rejmánek 2010	<i>Astrocarium mexicanum</i>	<i>Heteromys desmarestianus</i>	0.076	0.354	0.215	here, the ratio of germination probabilities represents p_c , the probability that seed is cached, regardless of its fate (see the text for details)

*with the exception of Klinger and Rejmánek (2010), emergence probabilities were based on artificial cache experiments (simulated scatterhoarding), not the actual action of scatterhoarders.

**when measuring seedling establishment in the fall rather than germination or emergence in the spring.

***in the study, seeds were buried at depths 1–9 cm, but we calculated \hat{p}_c using data on germination and survival of seeds buried at the depth of 1 cm because it closely corresponded to the average depth of *T. amoenus* seed caches.

hereafter use the symbol $\tilde{p}_C \equiv e_S/e_C$ to represent this minimum beneficial proportion of cached and uneaten seeds. Identifying this threshold value allows us to use commonly-reported emergence rates to evaluate the net outcome in relation to plausible values of the unmeasured proportion of seeds that are cached and uneaten. Using this threshold does not allow us to identify the exact value of p_C in natural populations; instead, it allows us to assess what values would lead to mutualism versus antagonism, and whether these values are realistic.

Following this reasoning, we use the \tilde{p}_C threshold to evaluate whether caching is likely to benefit plants, based on commonly available data on seedling emergence rates from cached and uncached seeds (Fig. 1). If \tilde{p}_C is very small, we can be confident that granivory is beneficial for plants. If \tilde{p}_C is unrealistically large (e.g. considerably larger than the proportion of cached seeds that were left uneaten in the few published studies that measured this parameter, Vander Wall 1994, 2002, Gómez et al. 2008), granivores may not benefit plant fitness, even if caching per se increases seedling emergence. Intermediate values of \tilde{p}_C could be used simply to infer that the net outcome will be relatively sensitive to variation in abundance or behavior of granivorous animals. Alternatively, it could be used to justify further mechanistic studies, if the direction of the outcome is important to understand in a particular context.

Application to plant–granivore studies

We found 14 studies that compared the probability of emerging as seedlings for seeds that were scatterhoarded and those that were not handled by animals (Table 1). For practical reasons, most of these comparisons consisted of experiments where seeds, protected from granivory (often with wire mesh cages), were either placed on the ground or buried in shallow (usually 0.5–6 cm) artificial caches. In addition to the overcoming the difficulty of locating actual caches, this experimental design allows researchers to isolate what would happen to seeds in the absence of animals, even though in some species that are adapted to seed caching granivores, ‘unburied seeds’ rarely occur in nature (Vander Wall 1992).

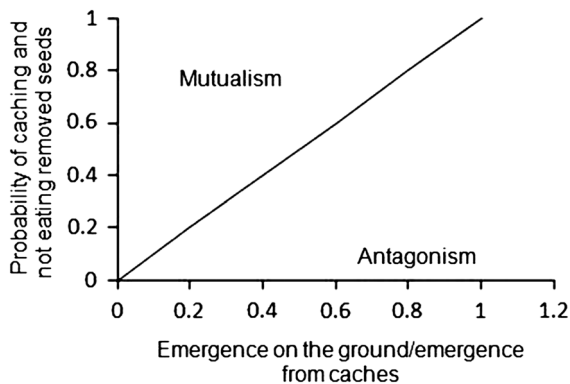


Figure 1. Classification of plant–granivore interactions based on the probability of caching and not eating removed seeds, and the ratio of seedling emergence from the ground to emergence from caches. The net effect of granivores is beneficial at any point above the line and antagonistic at any point below.

In three of these studies, unburied seeds did not emerge as seedlings (*Fagus sylvatica*, Jensen 1985; *Hymenaea courbaril*, Asquith et al. 1999; *Marab macrocarpus*, Borchert 2006; $\tilde{p}_C = 0$, Table 1). However, in most cases seed burial was beneficial but not necessary for emergence (Table 1). Using \tilde{p}_C as a relative measure of the likely benefits of granivore–plant interactions, the net effects ranged from situations where granivores were almost certainly beneficial to situations where their presence probably reduced plant recruitment (Table 1). For example, Vander Wall (1992) buried Jeffrey pine (*Pinus jeffreyi*) seeds 1 cm deep to simulate yellow pine chipmunk caches. He found that 55.2% of buried seeds emerged as seedlings, compared with only 0.9% of emergence when seeds were sown on soil or needle litter surface ($\tilde{p}_C = 0.016$). A later study in the same system (Briggs et al. 2009) confirmed this result although seedling emergence from soil was higher (4.7%), resulting in \tilde{p}_C of 0.154. Similarly, seed burial at depths corresponding to the depth of a typical rodent cache (10–50 mm) greatly increases the chances of seedling emergence in desert peach, *Prunus andersonii* (Beck and Vander Wall 2010) and antelope bitterbrush, *Purshia tridentata* (Vander Wall 199).

On the other end of the spectrum, seed burial had little effect on seedling emergence in *Gustavia superba* in a tropical moist forest of Panama (Sork 1985) and *Pinus coulteri* after a wildfire in California (Borchert et al. 2003). Almost 87% of handled seeds would have to be cached and never eaten by rodents to benefit the *G. superba* recruitment (Table 1); in the case of post-fire pine recruitment, the percentage was almost as high ($\tilde{p}_C = 0.747$, Table 1). Such values are unlikely (Vander Wall 2002), thus rodents probably exert a negative net influence on the recruitment in these tree species, even though many seedlings in burned forest established from rodent caches (Borchert et al. 2003). Similarly, Klinger and Rejmánek (2010) analyzed seed predation and dispersal in a tropical palm, *Astrocaryum mexicanum*. Dispersed seeds germinated almost five times better, resulting in minimum \tilde{p}_C of 0.215 (Table 1; see Appendix 2 for treatment of this study, which used a somewhat different experimental design). Klinger and Rejmánek (2010) estimated that on average, rodents cached only 9–13% of handled seeds (see their Table 3). This point estimate suggests that granivory is not beneficial for *Astrocaryum mexicanum*, in contrast to Klinger and Rejmánek’s conclusions, which were based on observing higher germination from caches than surface seeds. However, confidence estimates of germination rates were large, and include the possibility that granivory benefits palm recruitment in this system.

In the remaining studies, the role of granivory is more ambiguous: $\tilde{p}_C = 0.111$ in *Corylus avellana* (Kollmann and Schill 1996), 0.119 in *Quercus rubra* (Garcia et al. 2002), 0.156 in *Pinus ponderosa* (Keyes et al. 2009), 0.163 in *Quercus petraea* (Kollmann and Schill 1996), and 0.226 in *Pinus flexilis* (Tomback et al. 2005). Comparing these \tilde{p}_C values with data on survival of seeds handled by rodents in these (4.0–8.9% in *Pinus ponderosa*, Vander Wall 2002) or other plant species (1.4–12.7% in *Pinus jeffreyi* and *P. lambertiana*, Vander Wall 2002, approx. 10–16% in *Purshia tridentata*, Vander Wall 1994, Vander Wall and Joyner 1998, more than 1.3% in *Quercus ilex*, Gómez et al. 2008) suggests that seed dispersal by scatterhoarders could involve considerable costs.

However, it is possible that other benefits of scatterhoarding, beyond burial-related improvement in germination, determine that granivores do aid plant recruitment (Gómez et al. 2008).

Discussion

Our results weakly support the notion that plant–granivore interactions tend to be mutualistic. Of 14 study systems, six systems (seven studies) showed probable benefits to plants, three showed probable costs, and five systems (four studies) were ambiguous. They also strongly support the fact that the outcome differs among particular plant–granivore pairs and ecological situations. For example, disturbances that remove litter and competing vegetation often increase the probability of germination of seeds sown on the surface (Turnbull et al. 2000, Clark et al. 2007). Accordingly, among studies that we analyzed (Table 1) one of the highest \bar{p}_C values was in a study conducted in a burned forest (Borchert et al. 2003), indicating relatively little difference in germination on the surface and from caches and thus high costs of granivore foraging. It would be interesting to find out if the result that after disturbances granivores tend to adversely affect plant recruitment represents a more general pattern (Zwolak et al. 2010). In many cases, \bar{p}_C also varied among conditions within studies (Appendix 1). In most situations, these did not qualitatively change our conclusions, but in one case (Kollmann and Schill 1996) germination probabilities of both buried and unburied *Quercus* and *Coryllus* seed changed with the vegetation type, aspect, and the presence of mowing, and therefore \bar{p}_C varied widely within this system (Appendix 1).

Given this complexity, the main benefit of our approach may not be to obtain point estimates of \bar{p}_C for particular, often arbitrarily chosen, conditions. Instead, in our view, its main advantage is to provide a framework for investigating how different ecological conditions influence the balance between costs and benefits of scatterhoarding. For example, the propensity for caching depends on seed: scatterhoarder ratio (Theimer 2005). Seed abundance changes drastically e.g. in masting species: in non-mast years, scatterhoarders often consume most encountered seeds, possibly reducing plant recruitment, whereas in mast years scatterhoarders may be satiated and intensify caching, possibly improving recruitment (Theimer 2005). From our theoretical framework, we know that changing the proportion of seeds harvested does not influence the qualitative outcome of plant–granivore interactions. However, cache survival is also often higher in mast than in non-mast years, because animals tend to retrieve a smaller proportion of cached seeds (Theimer 2001, Vander Wall 2002, Jansen et al. 2004, but see Xiao et al. 2005). The closer the emergence ratio and \bar{p}_C threshold are to the proportion of cached and unrecovered seeds, the more likely it is that this difference would shift the qualitative outcome of the interaction.

In spite of its potential uses, there are a number of caveats to breaking down interactions into piecewise components. For example, estimates of \bar{p}_C might be influenced by the timing of comparison of performance of cached and uncached seeds. Most studies in Table 1 reported results based on counts of emerging seedlings (often, words ‘emergence’ and

‘germination’ were used interchangeably, Asquith et al. 1999, Keyes et al. 2009), but Vander Wall (1993) and Keyes et al. (2009) measured also seedling establishment in autumn. In both cases, the \bar{p}_C value was comparable but slightly lower than \bar{p}_C calculated on the basis of spring emergence (Table 1). Similarly, our analysis concentrates on relative improvements in germination probability that result from the action of granivores. Although most germination experiments listed in Table 1 focused only on the effects of burying seeds, consequences of scatterhoarding go beyond burial-related changes in germination probability. Other benefits and costs of scatterhoarding may include e.g. directed dispersal (Briggs et al. 2009), reducing the risk of consumption by naïve foragers (Brewer and Webb 2001), reducing density-dependent mortality near parent plants (Comita et al. 2010, Mangan et al. 2010), or damaging the plant embryo before caching (creating ‘zombie seeds’: Jansen et al. 2006). Moreover, in certain cases plant recruitment is limited by seedling rather than seed survival, and conditions that are beneficial to seeds are not necessarily beneficial to seedlings (Schupp 1995).

In certain environments, emergence from the surface might not adequately represent recruitment without granivores. Abiotic forces such as flooding or leaf fall might provide similar benefits to caching by scatterhoarding granivores without the cost of being eaten. However, some of such phenomena (e.g. leaf fall) can be simulated in simple experiments. In such cases, a proper comparison would involve e.g. germination from caches versus germination under leaves.

A final caveat is that our approach, like most of the studies we reviewed, assumes that plant–granivore interactions occur as isolated species pairs. In reality, plants interact with multiple granivores. For example, corvids might cache more *Pinus monophylla* seeds than rodents, but rodents probably bury the seeds in more favorable microsites (Chambers 2001). \bar{p}_C could be used as a metric to compare the effectiveness of different dispersal agents. Also, the general form of Eq. 1 suggests a framework for thinking about how the relative benefits of granivore interactions could change with changes in animal community composition. In a multispecies context, e_s could be replaced with background germination in the presence of all species except for a particular focal species. The marginal benefits of that focal species would then be determined by the ratio of seedling emergence with all species except the focal species versus from caches of the focal species. In the presence of relatively beneficial species, this ratio becomes larger, meaning it is harder for any given species to provide additional benefits, and in the presence of relatively antagonistic species, this ratio becomes smaller, meaning it is easier for a particular species to provide marginal benefits.

Past studies have reviewed plant–animal interactions that are more clearly mutualistic (ant–plant, plant–pollinator) or antagonistic (plant–herbivore). These studies have tended to conclude that, although there are some exceptions, interactions tend to be consistently mutualistic or antagonistic across ecological contexts (Morris et al. 2007, Chamberlain and Holland 2009). Relative to these examples, plant–granivore interactions have received less attention, possibly because they are less easy to classify as mutualistic versus antagonistic, or possibly because they initially seem to require overwhelming amounts of data to quantify (Schupp 1993,

Schupp et al. 2010). Our approach shows that preliminary inferences can be made with much less data, and that existing studies tend weakly towards mutualistic but highly context-dependent outcomes. It is not surprising that the qualitative outcome of plant–granivore interactions may be more context-dependent; indeed, it is rather comforting. Our approach also reveals which aspects of the interaction affect the direction of the outcome (mutualistic vs antagonistic), and which are only important for determining its exact magnitude. Finally, it provides a framework for evaluating when it is most necessary to measure the most difficult parameters, such as the proportion of seeds that are cached and uneaten. We hope that this kind of framework will make study of context-dependent interactions more efficient in general.

Acknowledgments – We would like to thank D. Levey and J. L. Bronstein for particularly helpful and insightful feedback on this manuscript. The work was conducted while R. Zwolak was supported by the MNiSW grant NN304 391 537 and the Foundation for Polish Science “Homings” fellowship, HOM/2009/16B, and while E. Crone was supported by a National Science Foundation research grant (DEB 05-15756).

References

- Agraval, A. A. et al. 2007. Filling key gaps in population and community ecology. – *Front. Ecol. Environ.* 5: 145–152.
- Asquith, N. M. et al. 1999. The fruits the agouti ate: *Hymenaea courbaril* seed fate when its disperser is absent. – *J. Trop. Ecol.* 15: 229–235.
- Beck, M. J. and Vander Wall, S. B. 2010. Seed dispersal by scatter-hoarding rodents in arid environments. – *J. Ecol.* 98: 1300–1309.
- Borchert, M. 2006. Seed fate of *Marahmacrocarpus* (Cucurbitaceae) following fire: do seedlings recruit from rodent burrows? – *Ecol. Res.* 21: 641–650.
- Borchert, M. et al. 2003. Early postfire seed dispersal, seedling establishment and seedling mortality of *Pinus coulteri* (D. Don) in central coastal California, USA. – *Plant Ecol.* 168: 207–220.
- Brewer, S. W. and Webb, M. A. H. 2001. Ignorant seed predators and factors affecting the seed survival of a tropical palm. – *Oikos* 93: 32–41.
- Briggs, J. S. et al. 2009. Forest rodents provide directed dispersal of Jeffrey pine seeds. – *Ecology* 90: 675–687.
- Bronstein, J. L. 1994. Conditional outcomes in mutualistic interactions. – *Trends Ecol. Evol.* 9: 214–217.
- Chamberlain, S. A. and Holland, J. N. 2009. Quantitative synthesis of context dependency in ant–plant protection mutualisms. – *Ecology* 90: 2384–2392.
- Chambers, J. C. 2001. *Pinus monophylla* establishment in an expanding *Pinus–Juniperus* woodland: environmental conditions, facilitation and interacting factors. – *J. Veg. Sci.* 12: 27–40.
- Clark, C. J. et al. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. – *Am. Nat.* 170:128–142.
- Comita, L. S. et al. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. – *Science* 329: 330–332.
- den Ouden, J. et al. 2005. Jays, mice and oaks: predation and dispersal of *Quercus robur* and *Q. petraea* in northwestern Europe. – In: Forget, P. M. et al. (eds), Seed fate. Predation, dispersal and seedling establishment. CABI Publishing, pp. 223–239.
- Forget, P. M. and Wenny, D. 2005. How to elucidate seed fate? A review of methods used to study seed removal and secondary seed dispersal. – In: Forget, P. M. et al. (eds), Seed fate. Predation, dispersal and seedling establishment. CABI Publishing, pp. 379–393.
- García, D. et al. 2002. Differential effects of acorn burial and litter cover on *Quercus rubra* recruitment at the limit of its range in eastern North America. – *Can. J. Bot.* 80: 1115–1120.
- Goheen, J. R. et al. 2010. Large herbivores facilitate savanna tree establishment via diverse and indirect pathways. – *J. Anim. Ecol.* 79: 372–382.
- Gómez, J. M. et al. 2003. Impact of vertebrate acorn- and seedling-predators on a Mediterranean *Quercus pyrenaica* forest. – *For. Ecol. Manage.* 180: 125–134.
- Gómez, J. M. et al. 2008. Effectiveness of rodents as local seed dispersers of Holm oaks. – *Oecologia* 155: 529–537.
- Holland, J. N. and Bronstein, J. L. 2008. Mutualism. – In: Jorgensen, S. E. (ed.), Encyclopedia of ecology. Elsevier, pp. 2485–2491.
- Hulme, P. E. and Kollmann, J. 2005. Seed predator guilds, spatial variation in post-dispersal seed predation and potential effects on plant demography: a temperate perspective. – In: Forget, P. M. et al. (eds), Seed fate. Predation, dispersal and seedling establishment. CABI Publishing, pp. 9–30.
- Jansen, P. A. and Forget, P. M. 2001. Scatterhoarding rodents and tree regeneration. – In: Bongers, F. et al. (eds), Dynamics and plant–animal interactions in a neotropical rainforest. Kluwer, pp. 275–288.
- Jansen, P. A. et al. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. – *Ecol. Monogr.* 74: 569–589.
- Jansen, P. A. et al. 2006. Tropical rodents change rapidly germinating seeds into long-term food supplies. – *Oikos* 113: 449–458.
- Jensen, T. S. 1985. Seed–seed predator interactions of European beech, *Fagus sylvatica* and forest rodents, *Clethrionomys glareolus* and *Apodemus flavicollis*. – *Oikos* 44: 149–156.
- Keyes, C. R. et al. 2009. Recruitment of ponderosa pine seedlings in the Cascade Range. – *For. Ecol. Manage.* 257: 495–501.
- Klinger, R. and Rejmánek, M. 2010. A strong conditional mutualism limits and enhances seed dispersal and germination of a tropical palm. – *Oecologia* 162: 951–963.
- Kollmann, J. and Schill, H. P. 1996. Spatial patterns of dispersal, seed predation and germination during colonization of abandoned grassland by *Quercus petraea* and *Corylus avellana*. – *Vegetatio* 125: 193–205.
- Mangan, S. A. et al. 2010. Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. – *Nature* 466: 752–755.
- Maron, J. L. and Simms, E. L. 1997. Effect of seed predation on seed bank size and seedling recruitment of bush lupine (*Lupinus arboreus*). – *Oecologia* 111: 76–83.
- Maron, J. L. and Crone, E. E. 2006. Herbivory: effects on plant abundance, distribution and population growth. – *Proc. R. Soc. B* 273: 2575–2584.
- Morris, W. F. et al. 2007. Direct and interactive effects of enemies and mutualists on plant performance: a meta-analysis. – *Ecology* 88: 1021–1029.
- Orrock, J. L. et al. 2008. Apparent competition with an exotic plant reduces native plant establishment. – *Ecology* 89: 1168–1174.
- Schupp, E. W. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. – *Vegetatio* 107/108: 15–29.
- Schupp, E. W. 1995. Seed–seedling conflicts, habitat choice, and patterns of plant recruitment. – *Am. J. Bot.* 82: 399–409.
- Schupp, E. W. et al. 2010. Seed dispersal effectiveness revisited: a conceptual review. – *New Phytol.* 188: 333–353.
- Sork, V. L. 1985. Germination response in a large-seeded neotropical tree species, *Gustavia superba* (Lecythidaceae). – *Biotropica* 17: 130–136.
- Theimer, T. C. 2001. Seed scatterhoarding by white-tailed rats: consequences for seedling recruitment by an Australian rain forest tree. – *J. Trop. Ecol.* 17: 177–189.

- Theimer, T. C. 2005. Rodent scatterhoarders as conditional mutualists.— In: Forget, P. M. et al. (eds), Seed fate. Predation, dispersal and seedling establishment. CABI Publishing, pp. 283–295.
- Tomback, D. F. et al. 2005. Life on the edge for limber pine: seed dispersal within a peripheral population. — *Écoscience* 12: 519–529.
- Turnbull, L. A. et al. 2000. Are plant populations seed-limited? A review of seed sowing experiments. — *Oikos* 88: 225–238.
- Vander Wall, S. B. 1992. The role of animals in dispersing a 'wind-dispersed' pine.— *Ecology* 73: 614–621.
- Vander Wall, S. B. 1993. A model of caching depth: implications for scatter hoarders and plant dispersal. — *Am. Nat.* 141: 217–232.
- Vander Wall, S. B. 1994. Seed fate pathways of antelope bitterbrush: dispersal by seed-caching yellow pine chipmunks. — *Ecology* 75: 1911–1926.
- Vander Wall, S. B. 2001. The evolutionary ecology of nut dispersal. — *Bot. Rev.* 67: 74–117.
- Vander Wall, S. B. 2002. Masting in animal-dispersed pines facilitates seed dispersal. — *Ecology* 83: 3508–3516.
- Vander Wall, S. B. and Joyner, J. W. 1998. Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow chipmunks (*Tamias amoenus*): potential effects on plant reproductive success. — *Can. J. Zool.* 76: 154–162.
- Vander Wall, S. B. et al. 2005. Seed removal, seed predation and secondary dispersal. — *Ecology* 86: 801–806.
- Xiao, Z. et al. 2005. The effects of seed abundance on seed predation and dispersal by rodents in *Castanopsis fargesii* (Fagaceae). — *Plant Ecol.* 177: 249–257.
- Zwolak, R. et al. 2010. Fire and mice: seed predation moderates fire's influence on conifer recruitment. — *Ecology* 91: 1124–1131.

Appendix 1

Ranges of emergence rates and changes in the resulting EQ1 index (representing the ratio of emergence probabilities of cached to uncached seeds) under different ecological conditions.

Study	e_s	e_c	\tilde{p}_c
Jensen 1985	0	0, 0.08 or 0.42 depending on plant community	0
Sork 1985	varied from 0.32 to 0.92 depending on forest age and microsite conditions	varied from 0.70 to 0.96 depending on forest age and microsite conditions	0.33–1.14
Vander Wall 1992	0.01 (1 out of 100 seeds) when seeds were left on the soil surface; 0.009 (1 out of 125) for seeds left on the litter surface	0.552	0.016–0.018
Vander Wall 1993	0.022	highest (0.626) when seeds were buried at 20 mm; declined with depth, reaching 0.005 at 60 mm and 0 at 100 mm.	0.035 when seeds were buried at 20 mm; increased with depth
Kollmann and Schill 1996	depending on vegetation type, 0.00–0.11 for <i>Corylus avellanus</i> and 0.04–0.034 for <i>Quercus petraea</i>	depending on vegetation type, 0.42–0.57 for <i>Corylus avellanus</i> and 0.79–0.96 for <i>Quercus petraea</i>	0.000–0.261 for <i>Corylus avellanus</i> and 0.04–0.354 for <i>Quercus petraea</i>
Garcia et al. 2002	averages from two sites: 0.090 without litter cover; 0.043 under litter cover	averages from two sites: 0.702 without litter cover; 0.412 under litter cover	0.128 in the absence of litter; 0.104 in the presence of litter
Borchert et al. 2003	0.768 in year 1997; 0.179 in 1998	0.768 in 1997; 0.5 in 1998	1.000 in 1997; 0.358 in 1998
Tomback et al. 2005	0.10	0.54 for seeds cached under plants (60% of cached seeds); 0.44 for seeds cached in soil (14%); 0 for seeds cached in litter (3%), 0.10 when seeds are cached on surface (23%)*	0.185 when seeds were cached under plants, 0.227 when seeds were cached in soil, 1 when seeds were cached on surface
Borchert 2006	0	0.51–0.67 depending on depth	0
Briggs et al. 2009	0.047	0.276 for seeds buried at 5 mm, 0.335 for seeds buried at 25 mm	0.140–0.170

*Tomback et al. (2005) classifies seeds removed by rodents but left unburied as 'cached on the surface': in this case by definition, $e_c = e_s$ and $\tilde{p}_c = 1$.

Appendix 2

Application of seed caching model to Klinger and Rejmánek (2010)

Klinger and Rejmánek (2010) analyzed seed predation and dispersal in a tropical palm, *Astrocaryum mexicanum*. In this study, the researchers compared germination probabilities of seeds that were dispersed by rodents *Heteromys desmarestianus* (regardless if caching consisted of leaving seeds on the surface or burying in the litter) and undispersed. Therefore, to interpret these results, we need to expand the terms in Eq. 3 to separate caching from predation of cached seeds:

$$\begin{aligned}
 e_S &< p_R p_K (1 - p_E) e_C + (1 - p_R) e_S \\
 &\downarrow \\
 e_S - (1 - p_R) e_S &< p_R p_K (1 - p_E) e_C \\
 &\downarrow \\
 (1 - 1 + p_R) e_S &< p_R p_K (1 - p_E) e_C \\
 &\downarrow \\
 e_S p_R &< p_R p_K (1 - p_E) e_C \quad (6) \\
 &\downarrow \\
 \frac{e_S p_R}{p_R e_C} &< p_K (1 - p_E) \\
 &\downarrow \\
 \frac{e_S}{e_C} &< p_K (1 - p_E) \\
 \frac{e_S}{e_C (1 - p_E)} &< p_K
 \end{aligned}$$

Where p_K is the probability a seed is cached p_E is the probability a cached seed is retrieved and eaten and, by definition, $p_C \equiv p_K (1 - p_E)$. Klinger and Rejmánek (2010) measured germination of seeds left on the surface (and protected from predation), e_S , and germination of cached seeds, rather than germination of buried seeds protected from predation, i.e., they measured $e_C (1 - p_E)$. Dispersed seeds germinated almost 5 times better, resulting in minimum p_K of 0.215. In the main discussion of our paper, we substitute the minimum p_K for \tilde{p}_C and use the appropriately match rate of caching, i.e. the percent of handled seeds that were cached.