Conditions favouring hard seededness as a dispersal and predator escape strategy

Torbjørn R. Paulsen[1]*, Göran Högstedt[1], Ken Thompson[2], Vigdis Vandvik[1] and Sigrunn Eliassen[1]

[1]*Department of Biology, University of Bergen, Postboks 7803, 5020 Bergen, Norway; and* [2]*Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK*

Summary

1. The water-impermeable seed coat of 'hard' seeds is commonly considered a dormancy trait. Seed smell is, however, strongly correlated with seed water content, and hard seeds are therefore olfactionally cryptic to foraging rodents. This is the rationale for the crypsis hypothesis, which proposes that the primary functions of hard seeds are to reduce seed predation and promote rodent seed dispersal.

2. We use a mechanistic model to describe seed survival success of plants with different dimorphic soft and hard seed strategies. The model is based on established empirical–ecological relationships of moisture requirements for germination and benefits of seed dispersal, and on experimentally demonstrated relationships between seed volatile emission, predation and predator escape.

3. We find that water-impermeable seed coats can reduce seed predation under a wide range of natural humidity conditions. Plants with rodent dispersed seeds benefit from producing dimorphic soft and hard seeds at ratios where the anti-predator advantages of hard seeds are balanced by the dispersal benefits gained by producing some soft seeds.

4. The seed pathway predicted from the model is similar to those of experimental seed-tracking studies. This validates the relevance and realism of the ecological mechanisms and relationships incorporated in the model.

5. *Synthesis*. Rodent seed predators are often also important seed dispersers and have the potential to exert strong selective pressures on seeds to evolve methods of avoiding detection, and hard seeds seem to do just that. This work suggests that water-impermeable hard seeds may evolve in the absence of a dormancy function and that optimal seed survival in many environments with rodent seed predators is obtained by plants having a dimorphic soft and hard seed strategy.

Key-words: dispersal, granivore, mechanistic model, olfaction, physical dormancy, rodent, seed predation

Introduction

Physical dormancy or hard seededness is the second most common type of dormancy world-wide. It has been found in 14% of all species with known dormancy status (2000 species from 20 families) and has been shown to be very common in many lineages in the Fabaceae, Cistaceae, Geraniaceae, Malvaceae, Rhamnaceae and Sapindaceae (Morrison *et al.* 1992; Thanos *et al.* 1992; Meisert 2002; Baskin & Baskin 2014). The trait is found across all plant growth forms, biomes and biogeographical regions and is particularly common in tropical deciduous forests, savannas, steppe, matorral and deserts, where it occurs in 20–40% of species (Baskin & Baskin 2014). The water impermeability of these seeds is caused by a specialized lignified palisade layer in the seed coat, a highly derived trait that has evolved repeatedly and relatively late in different lineages of flowering plants (Willis *et al.* 2014). The time of origin of water-impermeable seeds is unknown, but there is some fossil evidence indicating that they could have been present in the Anacardiaceae as early as the Early Eocene (>55 Mya), and they are hypothesized to have appeared in the Fabaceae, Malvaceae, Cistaceae, Rhamnaceae and Geraniaceae as key lineages of these families appeared during diversification events in the Late Eocene and Micocene (i.e. between 48 and 15 Mya; Baskin & Baskin 2014).

For at least a century, the primary function of the water-impermeable seed coats of many land plants, also known as 'hard seeds' or 'physical dormancy', has been linked to germination regulation. This seems reasonable since these seeds cannot absorb water and thus cannot germinate until the seed

*Correspondence author: E-mail: torbjorn.paulsen@bio.uib.no

coat is breached. The literature examining the ecology and ecophysiology of hard seeds is almost exclusively concerned with their dormancy function, with special emphasis on how the water-impermeable seed coat is acquired and broken, as summarized by Baskin & Baskin (2014).

An alternative hypothesis, derived from Vander Wall (2003), is that the primary function of water-impermeable seeds is linked to their ability to keep volatiles in rather than to keep water out. This 'crypsis hypothesis' is based on the ability of the water-impermeable seed coat to prevent imbibition and therefore to prevent the generation and release of the volatile compounds that rodents use to detect buried seeds (Paulsen *et al.* 2013). Rodents primarily detect seeds by olfaction and can easily find buried moist seeds but struggle to detect buried dry seeds (Howard & Cole 1967; Johnson & Jorgensen 1981; Vander Wall 1993b, 1995, 1998; Jorgensen 2001). Paulsen *et al.* (2013) experimentally demonstrated that hard seeds are olfactionally cryptic to a seed-harvesting rodent and that this allows them to escape predation.

The crypsis hypothesis offers a plausible explanation for the function and evolution of hard seeds, and it also makes sense of several otherwise puzzling features of such seeds, none of which make much sense in the context of a purely germination-regulating role (Paulsen *et al.* 2013). First, a dormancy role does not explain why hard seeds are absent from lineages with small seeds (Leishman & Westoby 1998; Šerá & Šerý 2004; Moles *et al.* 2005). This is easily explained by the crypsis hypothesis since large seeds are attractive and detectable to rodents, even when buried, whereas for small seeds, prey value is small and burial itself offers protection against predation (Hulme 1998). Second, while hard seededness is a very effective anti-predator trait, it functions only as long as the seed coat is intact and the seed remains olfactionally cryptic. This may explain why hard seeds rarely have any other type of dormancy or discriminating germination requirements; once the seed coat is broken, the typical hard seed germinates rapidly over a wide range of temperatures in both light and darkness (Grime *et al.* 1981; Thanos *et al.* 1992; Baskin & Baskin 2014). Third, as Baskin & Baskin (1998) ask: why did physical dormancy evolve in so many families with recalcitrant (desiccation-sensitive) seeds? The answer may be that the two traits are alternative anti-predator strategies adopted by species with large seeds. Recalcitrant seeds are large, germinate very quickly and allocate few resources to physical defence against predators. This is interpreted as a means of escape from predation by shortening the time window between dispersal and germination (Pritchard *et al.* 2004; Daws, Garwood & Pritchard 2005).

Seed-eating rodents occur in all biogeographical regions except the Antarctic and some islands in the Arctic Ocean (Nowak 1999). Many members of the families such as squirrels and chipmunks (Sciuridae), kangaroo rats and pocket mice (Heteromyidae), New World mice (Cricetidae), Old World rats and mice (Muridae) and agoutis and acouchis (Dasyproctidae) are known to scatter-hoard seeds (Vander Wall 1990). Australia has few scatter-hoarding small mammals [two marsupials and one rodent according to Forget & Vander Wall (2001)], but 13 of near 80 terrestrial herbivorous marsupials and 49 of 64 native rodents are known to include seeds in their diet (Nowak 1999).

Although olfactionally cryptic hard seeds reduce seed predation (Paulsen *et al.* 2013), seed dispersal benefits by rodents may also be evolutionary important and help explain the occurrence of hard seededness in plants. Scatter hoarders are seed predators that store one or a few seeds together in widely dispersed caches, while larder hoarders store all harvested seeds in one or a few large, closely spaced caches (Vander Wall 1990). From a seed dispersal perspective, scatter hoarding is more beneficial because germination and seedling establishment is better due to, for example reduced density-dependent seed mortality and/or predation (McAuliffe 1990; Vander Wall 1994; Pizo 1997; Forget, Kitajima & Foster 1999; Wenny 1999). Dispersal to microsites that favour seed germination and seedling establishment (Vander Wall 1993a; Pearson & Theimer 2004; Briggs, Vander Wall & Jenkins 2009) is also higher when distributed widely in small caches compared to large larders. However, rodents often have mixed food-storing strategies, and many chipmunks and squirrels (Sciuridae), kangaroo rats (*Dipodomys*) and pocket mice (*Perognathus*, *Heteromys*) store seeds both in larders in their burrows and in scattered surface caches (Vander Wall 1990). For a description of rodent seed dispersal of the two hard-seeded plants *Cercidium microphyllum* (yellow or foothill paloverde) and *Prosopis velutina* (velvet mesquite), see McAuliffe (1990) and Reynolds & Glendening (1949), respectively.

Here, we use a mechanistic model to study how seed dispersal and predator escape may affect the profitability of hard and soft seed morphs in hard-seeded plants. We focus on the effects of predation pressure from rodents on seeds detectable by smell and on survival rates of seedlings due to reduced parent–offspring competition following seed dispersal. While the plant may benefit from having rodents move seeds away from the close vicinity of the mother plant (Schupp 1993), these animals also cause high rates of seed loss due to predation (Howard & Cole 1967; Johnson & Jorgensen 1981; Vander Wall 1993b, 1995, 1998; Jorgensen 2001). The discovery that soft and hard seeds are harvested at different proportions from mixed caches suggests that each seed morph will experience different rates of predation and dispersal benefits (Paulsen *et al.* 2013). As a consequence, the two seed morphs may experience different seedling survival and germination success. The trade-off between dispersal benefits and predation may therefore result in different optimal plant strategies (soft:hard seed ratios) depending on environmental conditions such as humidity, predator pressure, benefits of dispersal and a possible cost of increased generation time for hard seeds. Our aim is to identify the range of ecological and environmental conditions under which hard seeds are favoured, and we also discuss other factors that may influence the optimal soft:hard seed ratios in plants.

Materials and methods

We use a mechanistic model to study the seed germination success of plants that differ in their ratio of hard and soft seed morphs. We follow the fate of seeds from an initial seed cache through multiple caching and re-caching events, paralleling the design of real-world seed-tagging experiments (Vander Wall & Joyner 1998; Jansen *et al.* 2002; Vander Wall 2002; Xiao, Jansen & Zhang 2006). Our model is a compilation of the ecological processes facing the seed as rodents harvest and re-cache seeds. The first process describes how water-permeable soft seeds imbibe and release volatiles, where the amount of volatiles released from a cache is a function of environmental humidity (Vander Wall 1993b) and the number of soft seeds in a cache (Geluso 2005; Vander Wall 2008). The second process describes how rodents use these volatiles as cues to locate the cache and to find individual seeds within the located cache (Paulsen *et al.* 2013). Once a cache has been located individual seeds face three outcomes, they are eaten, re-cached or neglected. The neglected seeds may germinate, with a probability depending on the level of humidity in the environment. Seed germination and seedling establishment may also be affected by dispersal, and we consider two extremes along a continuum from no dispersal benefits of the rodent re-caching to high seed dispersal benefits (i.e. where there is a strong parent–offspring conflict). Finally, processes such as costs and benefits of dormancy, morph-related seed death and predation from other seed predators may affect soft and hard seed morphs differently and lead to differences in relative germination probability of soft and hard seeds. These different processes are not modelled explicitly, but we include a variable describing the relative germination probability of soft and hard seeds to study how differences in relative germination probability may alter the optimal plant strategy.

ASSUMPTIONS

The model is based on the assumptions that (i) soft and hard seed morphs can be produced in ratios raging from all seeds being soft to all being hard (Morrison *et al.* 1992; Thanos *et al.* 1992; Meisert 2002), (ii) the probability of cache detection depends on the amount of volatiles emitted from seeds in a cache. We assume that seeds become detectable at relatively low seed water content (~8%) and that higher seed water content adds little to cache detectability (Vander Wall 1993b), (iii) seed morph removal from a harvested cache differs between soft and hard seed morphs, with soft seeds being harvested at higher rates (Paulsen *et al.* 2013), (iv) seed germination probability is a function of seed water content, with higher seed water contents needed for germination than for volatile emissions (Yu *et al.* 2008), (v) dispersal benefits and number of caching events are positively correlated initially, up to a point where further re-cachings do not confer additional dispersal benefits (Vander Wall & Joyner 1998), and (vi) for simplicity, we assume that seeds from different mother plants are not mixed within caches (Shaw 1934; McAdoo *et al.* 1983; but see also Vander Wall 2008).

THE MODEL

We consider the plant strategy s, which is the proportion of soft seeds produced by the plant (the remaining $1 - s$ being hard seeds). While hard seeds are impermeable to water, soft seeds will imbibe and start emitting volatiles when exposed to moisture (Paulsen *et al.* 2013). These compounds can be detected by rodent seed predators, and the amount of smell released from soft seeds depends on the humidity h in the environment (e.g. Vander Wall 1993b; Downs & Vander Wall 2009). We assume that smell increases with humidity according to $k_s = h^\beta$, in which β is a scaling factor (Table 1).

Seed predation and detection of caches

In dry environments ($h = 0$), no volatiles are released, and the probability of finding soft seeds equals the probability of detecting hard seeds (Paulsen *et al.* 2013). When humidity rises, hard and soft seeds morphs are found and removed by rodents in different proportions (Paulsen *et al.* 2013). The probability of a predator detecting a seed cache increases with the amount of volatiles released, which again is a function of the number of soft seeds in the cache (Geluso 2005; Vander Wall 2008) and of humidity. There is a baseline rate of seed detection, k_0, for both seed morphs that is independent of smell (e.g. due to random search or spatial memory). For simplicity, we assume that predators search randomly for caches within their preferred habitat and that the search efficiency is r. The probability that a predator will detect a cache during time interval t is then:

$$f(s,h) = 1 - \exp\left(-rtb(k_0 + sh^\beta)\right) \qquad \text{eqn 1}$$

where b is the number of seeds in the cache.

Once a seed cache is located, the predator harvests individual seeds within the cache. The probability that a seed is detected is positively correlated with seed smell and hence seed morph (Paulsen *et al.* 2013). In addition, a baseline detection probability accounts for other ways that the predators may find seeds in a located cache. The probability that an individual soft seed is detected is:

$$P_e^{SS} = 1 - \exp\left(-l(k_C + h^\beta)\right) \qquad \text{eqn 2}$$

and for a hard seed:

$$P_e^{HS} = 1 - \exp\left(-lk_C\right) \qquad \text{eqn 3}$$

Note that there is a different detection rate k_C for non-smelling seeds and different local search efficiency l when rodents search within the cache (Paulsen *et al.* 2013).

When the rodent finds a cache, it will eat a fraction of the seeds, re-cache some and neglect others (Vander Wall & Joyner 1998; Jansen *et al.* 2002; Vander Wall 2002; Xiao, Jansen & Zhang 2006). For a given cache event c, the total number of seeds found by the rodent is a combination of search efficiency first for locating a cache and second for locating individual seeds of both morphs within the cache. Thus, the number of soft seeds that remain in a cache is:

$$n_{SS}(c+1) = m_{SS}(c)\left[\exp\left(-rt(m(c)k_0 + m_{SS}(c)h^\beta)\right) + \left(1 - \exp\left(-rt(m(c)k_0 + m_{SS}(c)h^\beta)\right)\right)\exp\left(-l(k_C + h^\beta)\right)\right] \qquad \text{eqn 4}$$

and hard seeds:

$$n_{HS}(c+1) = m_{HS}(c)\left[\exp\left(-rt(m(c)k_0 + m_{SS}(c)h^\beta)\right) + \left(1 - \exp\left(-rt(m(C)k_0 + m_{SS}(c)h^\beta)\right)\right)\exp\left(-lk_C\right)\right] \qquad \text{eqn 5}$$

Table 1. Parameters and functions

	Description	Value
Parameter		
s	Proportion of soft seeds produced by a plant	[0,1]
h	Humidity in the environment	[0%, 100%]
c	Cache number	
b	Number of seeds in initial cache	10
k_0	Smell-independent detection factor in cache search	0.1
β	Factor scaling volatile emissions and environmental humidity	2.0
r	Predator search efficiency in cache search	0.7
l	Predator search efficiency for single seeds in cache	2.0
k_c	Smell-independent seed detection factor in local search	0.8
π	Proportion of seeds found in a cache that is eaten by a predator	0.15
G	Germination probability of hard seeds relative to soft seeds in the same cache	[0.1, 2.0]
a	Factor scaling relationship between seed survival success and distance from mother plant (caching event)	0.7
T	Scaling factor determining distance from the mother plant at which seed survival increases most rapidly	3.0
q	Factor that scales the relationship between seed survival and humidity	0.5
U	Scaling factor determining at which humidity seed survival increases the most	0.15
K	Uniform seed survival probability with distance from mother plant	0.2
Functions		
f	Cache detection probability	
K_s	Amount of volatiles emitted from soft seed	
P_e	Seed encounter probability for search within patch	
d	Seed survival success dependent of dispersal distance from mother plant (cache number)	
g	Seedling growth success as a function of humidity	
$n(c)$	Number of seeds remaining in cache c	
$m(c)$	Number of seeds re-cached from the cth cache	
$u(c)$	Number of seeds preyed upon at the cth caching event	
$w(c)$	Number of seeds from a given cache that germinates	
V	Plant fitness – total number of seeds that germinates successfully	

Here, $m = m_{SS} + m_{HS}$ is the number of seeds cached in the previous caching event c. The remaining seeds are either neglected (n), preyed upon (u) or re-cached once more:

$$m(c) = m(c-1) - n(c) - u(c) \qquad \text{eqn 6}$$

Initially, we start with a fixed number of seeds b cached together. The number of soft seeds $m_{SS}(0) = bs$, and for simplicity, we assume that predators do not mix seeds from different caches when re-caching as is the case, for example in heteromyids and muridae (Shaw 1934; McAdoo *et al.* 1983; Vander Wall 1990). As a consequence, the subsequent caches will be smaller and will contain a different proportion of hard and soft seeds than the original cache. We update the number of seeds following each caching event and find cache detection probabilities, predation rates, fractions of seeds that are neglected and re-caching probabilities for each seed morph.

Seed germination

The plant strategy is evaluated on the basis of the germination success of all the seeds that the plant produces. Germination success differs between seed morphs depending on rate of seed predation, dispersal benefits and seed germination probability as described above. For seeds escaping predation, we consider two scenarios that may represent extremes along a continuum of parent–offspring conflict. First, we assume that germination success is independent of seed dispersal, $d(c) = K$. This represents a situation where there is no parent–offspring conflict (e.g. for desert annuals). Next, we assume very high parent–offspring conflict and that germination success increases with dispersal benefits (Janzen 1970; Schupp 1993). We represent this process with a sigmoidal function assuming that the

first caching event gives limited dispersal benefits after which dispersal benefits increase and lead to higher germination success for intermediate numbers of caching events. Further dispersal due to re-caching will only lead to marginal additional benefits:

$$d(c) = \frac{1}{1 + \exp(-a(c-T))} \qquad \text{eqn 7}$$

Here, a is the steepness by which the probability that a seed will germinate successfully increases with number of caching events, and T is the point (caching number) at which this function increases most rapidly.

The probability that a seed will germinate also depends on the general humidity h of the environment. For a given environment, the probability that a seed will germinate increases as:

$$g(h) = \frac{1}{1 + \exp(-q(h-U))} \qquad \text{eqn 8}$$

where q gives the steepness and U the humidity at which the germination probability changes most rapidly. Note that the success of different plant strategies is found given a level of environmental humidity; hence, the probability that a seed germinates in this environment ($g(h)$) does not affect the plant strategy but only the relative success of seeds in different environments.

Optimal plant strategies

Given the number of seeds being cached c times, seedling success as a function of dispersal $d(c)$, the effect of humidity $g(h)$ and the number of seeds successfully germinating from a given cache is as follows:
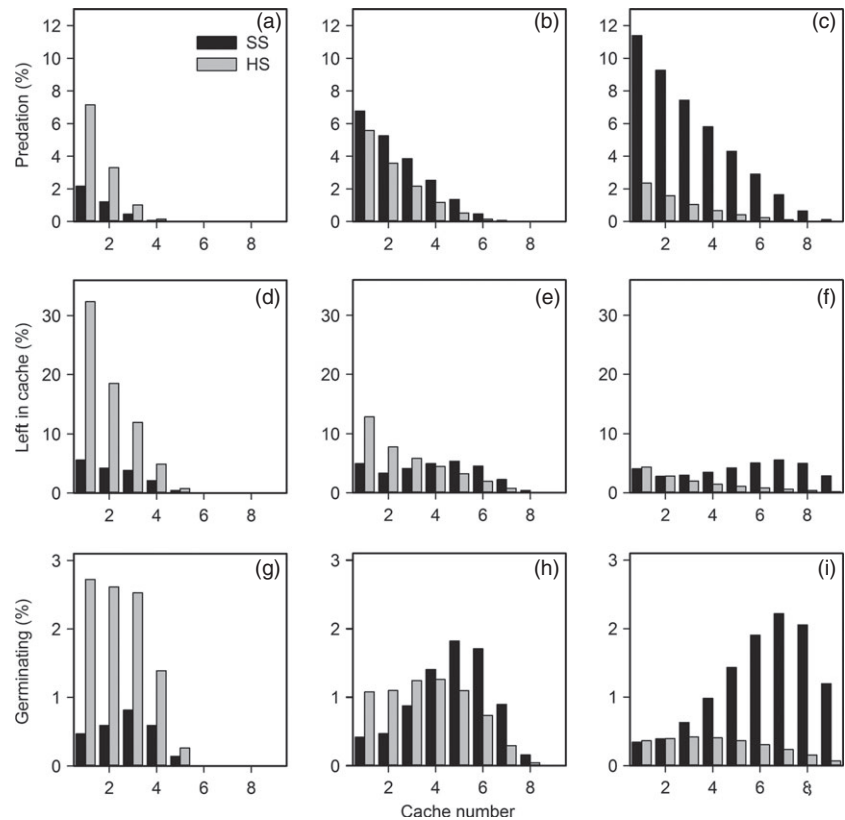
Fig. 1. Predicted seed pathways of modelled seeds. Effects of different soft:hard seed ratios (a,d,g: $s = 0.2$; b,e,h: $s = 0.5$; c,f,i: $s = 0.8$) on percentage of seeds preyed upon, neglected and germinating from each cache. Parameter values as in Table 1 with $h = 9\%$ and $G = 1.0$. Black bars: soft seeds (SS), grey bars: hard seeds (HS).

$$w(c|s) = d(c)g(h)(n_{SS}(c) + n_{HS}(c)G) \qquad \text{eqn 9}$$

Here, G is the relative seed germination probability of hard compared to soft seeds within the same cache (integrated over the time that the seeds may germinate). G is not related to rodent dispersal or predation but accounts for other factors that may affect germination of the two seed morphs differently. These factors include differences in local seedling competition within a cache, cost of increased generation time for hard seeds and seed survival benefits associated with physical dormancy in unpredictable environments. By exploring a continuum of G values, we can describe the combined result of these factors without knowing the exact effects that each factor has on seed morphs fitness.

For a plant that produces a proportion of soft seeds s, the total seed survival success of all seeds is the sum of seeds that germinate from every harvested cache c:

$$V(s|h, r) = \Sigma_{c=1}^{\infty} w(c|s) \qquad \text{eqn 10}$$

We use seedling success as the fitness criterion and calculate the optimal strategy s^* that results in maximum seedling establishment, given the predation pressure and humidity in the environment.

Results

The model predicts that differences in rodent predator pressure, environmental humidity and parent–offspring conflicts will result in different seed predation, dispersal and germination successes in plants with different dimorphic soft and hard seed morph strategies.

When there are more hard than soft seeds in the initial cache, we predict that a large proportion of seeds escapes predation, but these seeds are left to germinate relatively close to the mother plant (Fig. 1a,d,g, $s = 0.2$). When there are more soft than hard seeds, seed loss due to predation is predicted to be higher, but seed dispersal distance increases (Fig. 1c,f,i, $s = 0.8$). Many seeds, especially hard seeds, are neglected (Fig. 1f) and are re-cached only a few times. When the two seed morphs are produced in equal proportions, relative predation rates on soft seeds are predicted to be higher than for hard seeds (Fig. 1b, $s = 0.5$), but more hard seeds are neglected in caches closer to the mother plant (Fig. 1e, $s = 0.5$). When there are benefits of seed dispersal due to parent–offspring conflict, the proportion of seeds that successfully germinate is higher for seeds that are dispersed further from the mother plant (Fig. 1g–i). Consequently, we predict that there are more hard seeds germinating from the first caches, while soft seeds experience higher germination success away from the mother plant (Fig. 1h). The seed fate pathways predicted by the model are comparable to empirical observations from seed-tagging studies that examine post-dispersal seed fates (Table 2).

The model further predicts that different plant strategies are profitable under different humidity regimes (Fig. 2). When the environment is extremely dry, plants are predicted to produce a large fraction of soft seeds without experiencing a lot of predation (Fig. 2a). When humidity increases, the fraction of soft seeds drops off, and the predicted optimal plant strategy is to produce a mixture of soft and hard seed as long as there is a benefit of seed dispersal (Fig. 2).

The optimal soft:hard seed ratio for a plant is also predicted to depend on the relative dispersal benefits (strength of parent–offspring conflict) and relative seedling establishment
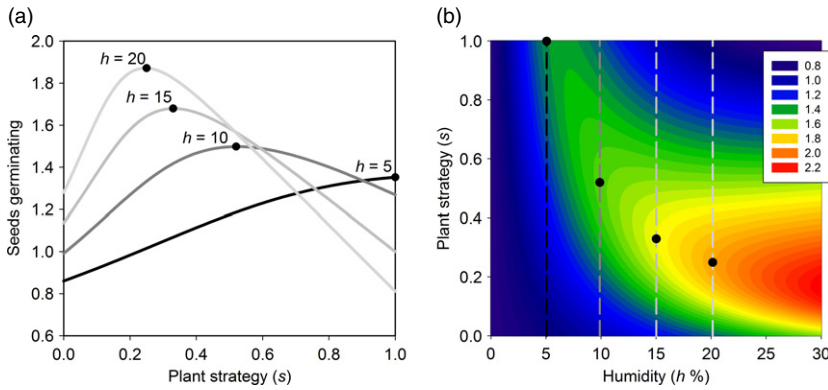
Fig. 2. Humidity and optimal soft:hard seed strategies. (a) Germination success as a function of plant strategy (*s;* soft seed proportion of total) for different levels of environmental humidity (*h*%). (b) The fitness landscape gives the number of seeds that germinate as a function of plant strategy and environmental humidity. Seed germination success increases from blue to red. For each humidity level, there is an optimum plant strategy marked with black dots, and the four humidity levels portrayed in (a) are represented by vertical lines in (b).
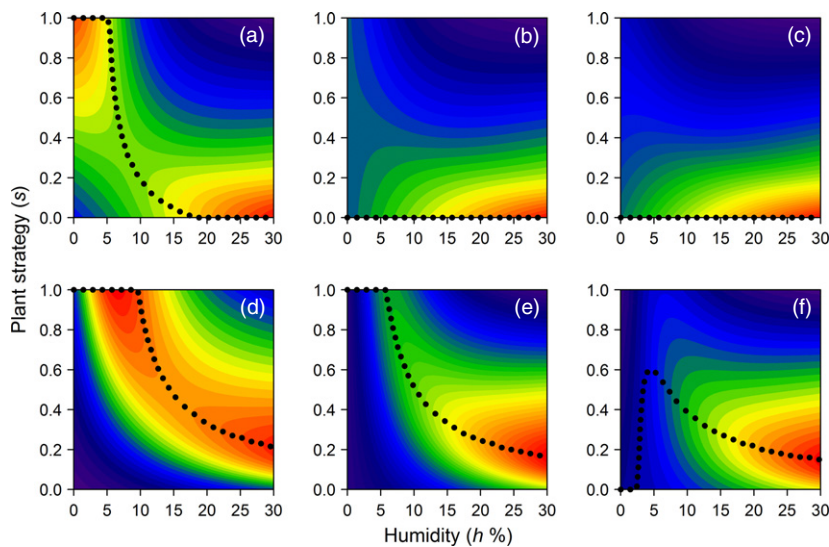

Fig. 3. Seed germination success as a function of plant strategy (*s;* soft seed proportion of total) and humidity (*h*%) in the environment. The black dotted lines give the optimal plant strategy given the environmental conditions and show the ridge in this topographic fitness landscape where fitness increases from blue to red. In (a–c), seed germination success is independent of dispersal benefits, while in (d–f), dispersal benefits (as a function of re-cachings) increases germination success. Every time a cache is located, the predator eats 15% of the seeds, neglects some and re-caches the rest. The model is run for three different relative fitness levels between the hard and soft morphs (due to factors unrelated to rodent seed dispersal and predation that affect germination of the two seed morphs differently, including generation time, non-rodent predation, etc., that is *G* is 0.5 (a,d), 1.0 (b,e) and 1.5 (c,f)). Other parameter values as in Table 1.

from hard and soft seeds caused by differences in seed predation, dispersal benefits and dormancy costs (Fig. 3). Without any dispersal benefits, the predicted plant strategy reflects the trade-off between predation escape of hard seeds and shorter generation times of soft seeds (Fig. 3a-c). In moderately dry to humid environments, lower predation rates are balanced against the longer generation time of hard seeds (Fig. 3a, *G* = 0.5). The optimal plant strategy is thus to produce dimorphic soft and hard seeds with the proportion of soft seeds reflecting the general soft seed advantage of shorter generation time in this scenario (Fig. 3a, *G* = 0.5). In extremely dry environments, we predict an all-soft strategy since the predation cost of being soft disappears when seed moisture levels are below the animal detection threshold (Fig. 3a, *G* = 0.5). In cases where there is an advantage to hard seeds that outweighs the general cost associated with longer generation times (e.g. physical dormancy benefits, *G* > 1.0),

the optimal plant strategy is to produce only hard seeds (Fig. 3b,c).

When there is a parent–offspring conflict and seed dispersal away from the mother plant is advantageous, we predict dimorphic seed strategies in most cases (Fig. 3d–f). When humidity and predation are low and relative soft seed germination success is higher than for hard seeds (Fig. 3d, *G* = 0.5) due to, for example, costs of increased generation time in hard seeds, we predict that plants benefits from producing a high proportion of soft seeds. At humidity levels when the seeds become olfactionally detectable by rodents, the proportion of soft seeds drops (Fig. 3d–f). Higher environmental humidity results in more soft seed predation, and the optimal seed ratio shifts towards higher proportions of hard seeds irrespective of *G* (Fig. 3d–f). When plants benefit from seed dispersal by rodents, we predict that producing some soft seeds may still be beneficial even when these seeds

Table 2. Seed fate pathway comparisons. Tracked seed fates of experimentally offered and modelled seeds that are either eaten or lost, neglected and left to germinate, or cached. The values given are percentages relative to the total number initially offered at a feeding station (100%). In the next re-caching event, the seeds again face the same fates, and seed fates are tracked and presented during subsequent re-cachings until all seeds are eaten/lost or neglected. For the modelled data, the fate pathways of hard and soft seeds are predicted together with the morph fractions given in brackets. The empirical pathway data were not used when constructing the model. *Pinus ponderosa* (Pp), *Carapa procera* (Cp), *Pinus jeffreyi* (Pj), *Pinus lambertiana* (Pl), *Camellia oleifera* (Co), *Quercus variabilis* (Qv)

Cache	Seeds	Pp*	Cp†	Pp‡	Pj‡	Pl‡	Pp‡	Pj‡	Pl‡	Pp‡	Pj‡	Pl‡	Co§	Qv§	Model (soft, hard)
1	Eaten/lost	24.3	35.2	17.0	44.3	35.5	59.4	42.0	34.8	31.2	22.7	30.2	30	52	32.1 (13.5, 18.7)
	Germinated	1.0	0	0	0	0	0	0	0	0	0	0	0	0	1.8 (0.6, 1.2)
	Seeds cached	74.7	64.8	83.0	55.7	64.5	40.6	58.0	65.2	68.8	77.3	69.8	70	48	66.1 (35.9, 30.2)
2	Eaten/lost	36.5	53.4	47.1	38.3	44.6¶	25.6	35.8	34.3	26.6	24.4	29.0	39	23	20.1 (9.3, 0.8)
	Germinated	9	2	3.2	1.1	6.0	7.7	6.6	9.6	1.5	0.4	0.6	8	17	1.9 (0.7, 1.2)
	Seeds cached	29.1	9.4	32.7	16.3	13.7	7.3	16.1	21.3	40.7	52.5	40.2	23	8	44.1 (25.9, 18.2)
3	Eaten/lost	17.5	8.4	26.8	13.8	9.8	5.9	13.0	17.8	19.4	24.8	22.7	14	5	15.1 (8.0, 7.1)
	Germinated	2.2	0.2	5.5	1.0	3.6	0.6	1.9	2.7	1.9	0.6	0.6	6	3	2.6 (1.3, 1.3)
	Seeds cached	9.4	0.8	0.4	1.5	0.2	0.8	1.2	0.8	19.4	27.1	16.9	3		26.4 (16.6, 9.8)
4	Eaten/lost	7.1	0.8	0.2	1.5	0.2	0.8	1.0	0.4	12.5	19.2	11.3	1		10.6 (6.3, 4.3)
	Germinated	1.0		0.2				0.2	0.4	0.4	0.4	0.2	2		3.1 (1.8,1.3)
	Seeds cached	1.3								6.5	7.5	5.4			12.7 (8.5, 4.2)
5	Eaten/lost	0.9								5.4	6.0	4.6			6.3 (4.1,2.2)
	Germinated	0.4													2.6 (1.7, 0.9)
	Seeds cached									1.1	1.5	0.8			3.8 (2.7, 1.1)
6	Eaten/lost									0.9	1.3	0.8			2.2 (1.5,0.7)
	Germinated									0.2					1.2 (0.8, 0.4)
	Seeds cached										0.2				0.4 (0.3, 0.1)
7	Eaten/lost										0.2				0.3 (0.2,0.1)
	Germinated														0.1 (0.1, 0)
	Seeds cached														

*Vander Wall & Joyner (1998),
†Jansen *et al.* (2002),
‡Vander Wall (2002),
§Xiao, Jansen & Zhang (2006),
¶value back calculated as the sum of germinated, eaten or lost, or re-cached seeds in cache 2. Published value is 80.3%.

have low relative germination success (Fig. 3f, $G = 1.5$). We suggest that soft seeds may then function as 'bait' for the predator and facilitate dispersal away from the mother plant.

The dimorphic strategy is robust to numerical changes to predator search efficiency (r) and relative seed germination success (G) (see Fig. S1 in Supporting Information).

Discussion

We suggest that plants should trade seed dispersal benefits against costs of seed predation by producing a mixture of hard and soft seeds when exposed to granivore rodents. In very dry environments, none of the seed types smell, and hence, the relative germination probability (G) of hard versus soft seeds determines the optimal seed morph strategy. At humidities where soft seeds start to release volatiles and become olfactionally detectable to rodents, a high soft seed ratio is predicted due to benefits of seed dispersal. With increasing humidity in the environment, the model predicts that plants benefit from producing more hard seeds to counter the increasing levels of predation. Conditions favouring a dimorphic soft:hard seed strategy are found under a wide range of environmental humidity levels, predator regimes and both low and high dispersal benefits. Even when hard seeds have higher relative germination probability than soft seeds,

our model suggests that producing some soft seeds is beneficial in the presence of seed dispersing granivores. As hard seeds are good at escaping seed predation (Reynolds & Glendening 1949; McAuliffe 1990; Paulsen *et al.* 2013), our results imply that this seed morph may evolve even in the absence of a dormancy function under a variety of environmental conditions.

Our model is based on the assumption that hard-seeded plants produce soft and hard seed morphs in variable proportions (assumption i). Lineages with hard-seeded plants contain everything from species without dormancy via dimorphic species to species that produce only hard water-impermeable seeds (Thanos *et al.* 1992). The fraction of dimorphic hard and soft seeds produced has been shown to vary among genotypes and lineages and to have a hereditary component (reviewed in Baskin & Baskin 2014, p. 278–279) and thus has the potential to respond adaptively to increase seed dispersal and/or reduce seed predation. While the overall prevalence of the seed permeability dimorphism is not well known, Baskin & Baskin (2014) list 166 species from families with dimorphic hard and soft seeds, for example in a number of species of *Acacia* of the tropics and dry subtropics, many species of *Lupinus* and *Trifolium* of temperate grasslands and mountains, and in important crops such as soya bean (*Glycine max*) and upland cotton (*Gossypium hirsutum*). However, this number is probably a

major underreporting of dimorphic species as soft:hard seed dimorphism was found in 40 of 42 investigated species of Old World Cistaceae (Thanos *et al.* 1992), in 27 of 35 Geraniaceae species from northern Germany, the Canary Islands and South Africa (Meisert 2002) and in all 34 of the Australian Faboideae and Mimosoideae species examined by Morrison *et al.* (1992), amounting to a total of 101 of 111 species examined for these 3 families alone. The corresponding numbers of species producing only (i.e. 100%) water-impermeable hard seeds are 2, 4 and 0, respectively. This underreporting of soft:hard dimorphism seems to be a consequence of the practices of scoring dormancy in broad classes (e.g., seedlots with >50% germination in untreated seeds scored as non-dormant; Baskin & Baskin 2014) and of routinely scarifying seeds of hard-seeded plant families prior to germination and viability testing (e.g. Millennium Seed Bank protocols prior to 2012).

We also assume (assumption ii) that the probability of cache detection depends on the amount of volatiles emitted from the seeds in a cache and that the strength of the volatile cue also depends on the number of soft seeds in a cache. Mature 'soft' seeds of most plants are very hygroscopic and readily absorb water making them olfactionally detectable to rodents across a wide range of moisture conditions (Shaw 1934; Howard & Cole 1967; Johnson & Jorgensen 1981; Vander Wall 1991, 1993b, 1995, 1998, 2000, 2003; Jorgensen 2001; Hollander, Vander Wall & Longland 2012). Rodents can detect seeds by smell at very low seed water content (~8%), and higher seed water content adds little to seed detectability (Vander Wall 1993b). Precipitation is not required, even high relative air humidity (95%), assumed to produce dew and increase soil water vapour, was enough to make buried *Pinus jeffreyi* (Jeffrey pine) seeds olfactionally detectable for *Tamias amoenus* (yellow pine chipmunks) while relative air humidities between 17 and 75% were not (Downs & Vander Wall 2009). The detectability of a single seed by rodents is thus almost an on/off switch strongly correlated to this seed water threshold, but the detectability of a cache is also dependent on the number of smelling seeds in a cache (Geluso 2005; Vander Wall 2008). We assume that the more smelly seeds there are in a cache, the higher the emission of volatiles will be and the farther away the rodent should be able to pick up the cue of a cache. In addition, in many systems, the humidity fluctuates, and a cache containing many soft seeds is expected both to become detectable more quickly as humidity increases and to dry out again more slowly than a cache with few imbibed seeds, increasing the time such a cache is olfactionally detectable to rodents.

The assumption (assumption iii) that seed morph removal from a harvested cache differs between soft and hard seed morphs is based on the only experiment, to our knowledge, that examines seed removal from caches containing both hard and soft seed morphs. When testing mixed caches containing 10 imbibed soft seeds and 10 hard seeds, Paulsen *et al.* (2013) found that hard seed harvest rates were around 25% lower than soft seeds for both *Robinia pseudoacacia* (black locust) and *Vicia sativa* (common vetch). Also, when hamsters were offered caches containing only imbibed or dry seeds, the cache detection rate was much higher for the soft seed morph, but once a cache was located, the hamsters harvested most of the hard seeds as well (Paulsen *et al.* 2013). The difference in seed removal of soft and hard seeds from mixed caches suggests different scatter-hoarding seed dispersal potentials for these seed morphs. In addition, neglected olfactionally cryptic hard seeds are very hard to find for seed predators and should benefit from seed dispersal and topsoil burial (Reynolds & Glendening 1949; McAuliffe 1990; Paulsen *et al.* 2013).

Seed water content required for germination varies greatly between seeds, but seeds start to smell at seed water contents below that needed for germination (assumption iv). For instance, Yu *et al.* (2008) found that seed moisture content at 50% loss of seed viability in eight non-pioneer tree species in a seasonal tropical rain forest in China varied from 12.4 to 42.5%. This means that seeds are especially vulnerable to predation at humidities where they have started to smell but are unable to germinate. We thus incorporate in the model that the probability of escaping predation by germination is higher in moist environments compared to dry environments.

We use caching events as a proxy for dispersal benefits, assuming that re-caching increases dispersal benefits, at least up to a point (assumption v). Although dispersal distances will vary with both rodent and plant species, caching and re-caching have the potential to increase dispersal distance. For instance, yellow pine chipmunks often placed primary caches under mother plants, and subsequent re-cachings redistribute seeds further away from the mother plant. In a seed-tagging experiment where the fates of individual seeds were followed, mean dispersal distance increased from 29.7 to 33.2, 36.8 and 38 m as seeds were re-cached up to 4 times (Vander Wall & Joyner 1998). Furthermore, dispersal benefits not only include escaping the mother plant, but also reduced sibling competition and the potential of ending up in a favourable microsite (McAuliffe 1990; Vander Wall 1993a, 1994; Pizo 1997; Forget, Kitajima & Foster 1999; Wenny 1999; Pearson & Theimer 2004; Briggs, Vander Wall & Jenkins 2009), both of which arguably increases with the first few caching events before additional caching adds little or no extra benefits. We therefore argue that using caching events as a proxy for dispersal benefits (allowing nonlinear relationships) incorporates a range of ecologically important dispersal benefits.

In the interest of model simplicity, we assume (assumption vi) that the hoarder does not mix seeds from different plants, as described, for example in heteromyids and muridae (Shaw 1934; McAdoo *et al.* 1983; McAuliffe 1990; Vander Wall 1990). However, seed mixing is probably also common (Vander Wall 2008), and this may influence optimal soft:hard seed ratios. If hard seeds are cached with soft seeds from a different plant, dimorphic plants may benefit from increasing their hard seed ratio and 'parasitize' the suggested dispersal advantage of soft seeds provided by other plants. The level of competition among plants for dispersal benefits may therefore depend on plant community and predator behaviour in a complex way and alter optimal soft:hard seed ratio even under similar environmental conditions. It is beyond the scope of

the present paper to examine this in detail, but we argue that although this has the potential to influence optimal hard:soft seed ratios in plants, it should not alter the general dynamics as described by the model.

The predicted seed fate pathway from the model mirrors those reported in seed-tagging experiments under natural conditions (Table 2), although the predicted cache sizes and the numbers of caching events are slightly higher than under natural conditions. This difference is expected; in the model, we keep track of all seeds until they are either eaten or germinate, while a substantial fraction of seeds is lost during caching and re-caching in field studies. Vander Wall & Joyner (1998), for instance, lost track of an increasing proportion of seeds, from 17.2% via 43.7%, 50.2%, 62.0% to 61.5%, as they were cached 1–5 times, respectively. We argue that the similarity between the predicted seed pathways based on mechanistic relationships of the model and experimental seed-tracking observations is a good validation of the representation of ecological processes in the model.

OTHER FACTORS INFLUENCING SEED MORPH RATIOS

Research on physically dormant seeds has mainly focused on hard seededness as a dormancy trait and more specifically on mechanisms releasing the seed from this dormancy, thus allowing germination at the right time and place for seedling establishment (Baskin & Baskin 2000). In many species, abiotic environmental conditions, such as high or low temperatures, high temperature fluctuations, drying at high temperature, incubation in wet warm conditions or exposure to fire, will make the seed coat permeable to water (Baskin & Baskin 1998; van Klinken, Lukitsch & Cook 2008). Many hard-seeded species have specialized anatomical features, such as the lens (strophiole) (Leguminosae), the bixoid chalazal apparatus (Malvales), the imbibition lid (Cannaceae) or the carpellary micropyle in endocarp of fruits of *Rhus* (Anacardiaceae), which are known to serve as environmental signal detectors (Baskin & Baskin 1998; Li, Baskin & Baskin 1999; Baskin, Baskin & Li 2000) allowing seed coats to admit water at times and places where seedling survival is high. These responses and adaptations also make sense from the crypsis hypothesis point of view. For the seed to germinate, the seed coat must become water permeable at some point, and any structures synchronizing this to times or places where germination and seedling survival are heightened will reduce the cost of increased generation time in olfactionally cryptic hard seeds. For instance, van Klinken, Lukitsch & Cook (2008) argued that physical dormancy in *Parkinsonia aculeate* (Jerusalem thorn or Mexican paloverde) functions not as a bet-hedging strategy, but as a mechanism maximizing seedling establishment by ensuring that germination coincides with conditions optimal for seedling establishment. This entails that in hard-seeded species, the presence of any adaptation that reduces the cost of hard seededness is expected to shift the soft:hard seed ratio towards higher hard seed fractions than in species without such a structure, all else being equal.

Under a wide range of environmental conditions, we predict that plants benefit from producing dimorphic hard and soft seeds. Why, then, is hard seededness found in only 14% (2000 plant species) of the species in which germination-regulating mechanisms have been studied (Baskin & Baskin 2014)? The answer might be that there are at least three alternative mechanisms by which plants may reduce seed predation and still use rodents for seed dispersal. First, many plant species produce secondary compounds that have a defensive role against seed predators (e.g. Bennett & Wallsgrove 1994) thus manipulating seed recovery of cached seeds by reducing seed prey value (Vander Wall 2010). Second, recalcitrant seeds (i.e. desiccation-sensitive) do not form even short-term soil seed banks. These seeds are shed and dispersed in the wet season when soil moisture levels favour rapid seed germination (Pritchard *et al.* 2004; Daws, Garwood & Pritchard 2005), which reduces the time window when they are available to seed predators. Third, masting, when a plant floods the predator populations with surplus food in some years, also allows plants to produce only soft seeds but still use scatter-hoarding animals for seed dispersal (Vander Wall 2010). In addition, the size of seeds that a rodent will harvest varies with size. If seeds are very small or large, they are not valued prey and generally escape rodent predation (Vander Wall 2010).

We predict that plants using scatter-hoarding rodents for seed dispersal should produce dimorphic soft and hard seed morphs under a wide range of predation pressures and natural humidity conditions and that water-impermeable hard seeds are expected to evolve under a variety of conditions even in the absence of a dormancy function. However, before we can critically evaluate the generality of the crypsis hypothesis, we need a better understanding of hard seeds as a seed dispersal and predator escape strategy from all biomes and biogeographical regions: We need precise information on soft and hard seed morph ratios in dimorphic plants, how these ratios vary between species and populations of species, how these ratios are regulated (biochemical regulation, and is it genetic or plastic?) and seed path studies to examine how the soft and hard seed morphs are treated by rodents in natural systems.

Acknowledgements

References

Baskin, C.C. & Baskin, J.M. (1998) *Seeds – Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego, CA.

Baskin, J.M. & Baskin, C.C. (2000) Evolutionary considerations of claims for physical dormancy-break by microbial action and abrasion by soil particles. *Seed Science Research*, **10**, 409–413.

Baskin, C.C. & Baskin, J.M. (2014) *Seeds, Ecology, Biogeography, and Evolution of Dormancy and Germination*, 2nd edn. Academic Press, San Diego, CA.

Baskin, J.M., Baskin, C.C. & Li, X. (2000) Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biology*, **15**, 139–152.

Bennett, R.N. & Wallsgrove, R.M. (1994) Tansley Review No. 72. Secondary metabolites in plant defence mechanisms. *New Phytologist*, **127**, 617–633.

Briggs, J.S., Vander Wall, S.B. & Jenkins, S.H. (2009) Forest rodents provide directed dispersal of Jeffrey pine seeds. *Ecology*, **90**, 675–687.

Daws, M.I., Garwood, N.C. & Pritchard, H.W. (2005) Traits of recalcitrant seeds in a semi-deciduous tropical forest in Panamá: some ecological implications. *Functional Ecology*, **19**, 874–885.

Downs, C.J. & Vander Wall, S.B. (2009) High relative humidity increases pilfering success of yellow pine chipmunks. *Journal of Mammalogy*, **90**, 796–802.

Forget, P.-M., Kitajima, K. & Foster, R.B. (1999) Pre- and post-dispersal seed predation in *Tachigali versicolor* (Caesalpiniaceae): effects of timing of fruiting and variation among trees. *Journal of Tropical Ecology*, **15**, 61–81.

Forget, P.-M. & Vander Wall, S.B. (2001) Scatter-hoarding rodents and marsupials: convergent evolution on diverging continents. *Trends in Ecology & Evolution*, **16**, 65–67.

Geluso, K. (2005) Benefits of small-sized caches for scatter-hoarding rodents: influence of cache size, depth, and soil moisture. *Journal of Mammalogy*, **86**, 1186–1192.

Grime, J.P., Mason, G., Curtis, A.V., Rodman, J. & Band, S.R. (1981) A comparative study of germination characteristics in a local flora. *Journal of Ecology*, **69**, 1017–1059.

Hollander, J.L., Vander Wall, S.B. & Longland, W.S. (2012) Olfactory detection of caches containing wildland versus cultivated seeds by granivorous rodents. *Western North American Naturalist*, **72**, 339–347.

Howard, W.E. & Cole, R.E. (1967) Olfaction in seed detection by deer mice. *Journal of Mammalogy*, **48**, 147–150.

Hulme, P.E. (1998) Post-dispersal seed predation and seed bank persistence. *Seed Science Research*, **8**, 513–519.

Jansen, P.A., Bartholomeus, M., Bongers, F., Elzinga, J.A., Ouden, J.D. & Van Wieren, S.E. (2002) The role of seed size in dispersal by a scatter-hoarding rodent. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 209–225. CABI Publishing, New York, NY.

Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *The American Naturalist*, **104**, 501–528.

Johnson, T.K. & Jorgensen, C.D. (1981) Ability of desert rodents to find buried seeds. *Journal of Range Management*, **34**, 312–314.

Jorgensen, E.E. (2001) Emission of volatile compounds by seeds under different environmental conditions. *American Midland Naturalist*, **145**, 419–422.

van Klinken, R.D., Lukitsch, B. & Cook, C. (2008) Interaction between seed dormancy-release mechanism, environment and seed bank strategy for a widely distributed perennial legume, *Parkinsonia aculeata* (Caesalpinaceae). *Annals of Botany*, **102**, 255–264.

Leishman, M.R. & Westoby, M. (1998) Seed size and shape are not related to persistence in soil in Australia in the same way as in Britain. *Functional Ecology*, **12**, 480–485.

Li, X., Baskin, J.M. & Baskin, C.C. (1999) Anatomy of two mechanisms of breaking physical dormancy by experimental treatments in seeds of two North American *Rhus* species (Anacardiaceae). *American Journal of Botany*, **86**, 1505–1511.

McAdoo, J.K., Evans, C.C., Roundy, B.A., Young, J.A. & Evans, R.A. (1983) Influence of heteromyid rodents on *Oryzopsis hymenoides* germination. *Journal of Range Management*, **36**, 61–64.

McAuliffe, J.R. (1990) Paloverdes, pocket mice, and bruchid beetles: interrelationships of seeds, dispersers, and seed predators. *The Southwestern Naturalist*, **35**, 329–337.

Meisert, A. (2002) Physical dormancy in Geraniaceae seeds. *Seed Science Research*, **12**, 121–128.

Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B. & Westoby, M. (2005) A brief history of seed size. *Science*, **307**, 576–580.

Morrison, D.A., Auld, T.D., Rish, S., Porter, C. & McClay, K. (1992) Patterns of testa-imposed seed dormancy in native Australian legumes. *Annals of Botany*, **70**, 157–163.

Nowak, R.M. (1999) *Walker's Mammals of the World*, 6th edn. Johns Hopkins University Press, Baltimore, MA.

Paulsen, T.R., Colville, L., Kranner, I., Daws, M.I., Högstedt, G., Vandvik, V. & Thompson, K. (2013) Physical dormancy in seeds: a game of hide and seek? *New Phytologist*, **198**, 496–503.

Pearson, K. & Theimer, T. (2004) Seed-caching responses to substrate and rock cover by two *Peromyscus* species: implications for pinyon pine establishment. *Oecologia*, **141**, 76–83.

Pizo, M.A. (1997) Seed dispersal and predation in two populations of *Cabralea canjerana* (Meliaceae) in the Atlantic Forest of southeastern Brazil. *Journal of Tropical Ecology*, **13**, 559–577.

Pritchard, H.W., Daws, M.I., Fletcher, B.J., Gaméné, C.S., Msanga, H.P. & Omondi, W. (2004) Ecological correlates of seed desiccation tolerance in tropical African dryland trees. *American Journal of Botany*, **91**, 863–870.

Reynolds, H.G. & Glendening, G.E. (1949) Merriam kangaroo rat a factor in mesquite propagation on southern Arizona range lands. *Journal of Range Management*, **2**, 193–197.

Schupp, E. (1993) Quantity, quality and the effectiveness of seed dispersal by animals. *Vegetatio*, **107–108**, 15–29.

Šerá, B. & Šerý, M. (2004) Number and weight of seeds and reproductive strategies of herbaceous plants. *Folia Geobotanica*, **39**, 27–40.

Shaw, W.T. (1934) The ability of the giant kangaroo rat as a harvester and storer of seeds. *Journal of Mammalogy*, **15**, 275–286.

Thanos, C.A., Kyriacos, G., Kadis, C. & Pantazi, C. (1992) Cistaceae: a plant family with hard seeds. *Israel Journal of Botany*, **41**, 251–263.

Vander Wall, S.B. (1990) *Food Hoarding in Animals*. University of Chicago Press, Chicago, IL.

Vander Wall, S.B. (1991) Mechanisms of cache recovery by yellow pine chipmunks. *Animal Behaviour*, **41**, 851–863.

Vander Wall, S.B. (1993a) Cache site selection by chipmunks (*Tamias spp.*) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*). *Oecologia*, **96**, 246–252.

Vander Wall, S.B. (1993b) Seed water content and the vulnerability of buried seeds to foraging rodents. *American Midland Naturalist*, **129**, 272–281.

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. (1995) Influence of substrate water on the ability of rodents to find buried seeds. *Journal of Mammalogy*, **76**, 851–856.

Vander Wall, S.B. (1998) Foraging success of granivorous rodents: effects of variation in seed and soil water on olfaction. *Ecology*, **79**, 233–241.

Vander Wall, S.B. (2000) The influence of environmental conditions on cache recovery and cache pilferage by yellow pine chipmunks (*Tamias amoenus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology*, **11**, 544–549.

Vander Wall, S.B. (2002) Masting in animal-dispersed pines facilitates seed dispersal. *Ecology*, **83**, 3508–3516.

Vander Wall, S.B. (2003) How rodents smell buried seeds: a model based on the behavior of pesticides in soil. *Journal of Mammalogy*, **84**, 1089–1099.

Vander Wall, S.B. (2008) On the relative contributions of wind vs. animals to seed dispersal of four Sierra Nevada pines. *Ecology*, **89**, 1837–1849.

Vander Wall, S.B. (2010) How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365**, 989–997.

Vander Wall, S.B. & Joyner, J.W. (1998) Reaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): potential effects on plant reproductive success. *Canadian Journal of Zoology*, **76**, 154–162.

Wenny, D.G. (1999) Two-stage dispersal of *Guarea glabra* and *G. kunthiana* (Meliaceae) in Monteverde, Costa Rica. *Journal of Tropical Ecology*, **15**, 481–496.

Willis, C.G., Baskin, C.C., Baskin, J.M., Auld, J.R., Venable, D.L., Cavender-Bares, J., Donohue, K., de Casas, R.R. & The NESCent Germination Working Group (2014) The evolution of seed dormancy: environmental cues, evolutionary hubs, and diversification of the seed plants. *New Phytologist*, **203**, 300–309.

Xiao, Z., Jansen, P.A. & Zhang, Z. (2006) Using seed-tagging methods for assessing post-dispersal seed fate in rodent-dispersed trees. *Forest Ecology and Management*, **223**, 18–23.

Yu, Y., Baskin, J., Baskin, C., Tang, Y. & Cao, M. (2008) Ecology of seed germination of eight non-pioneer tree species from a tropical seasonal rain forest in southwest China. *Plant Ecology*, **197**, 1–16.

Supporting Information

Additional Supporting Information may be found in the online version of this article:
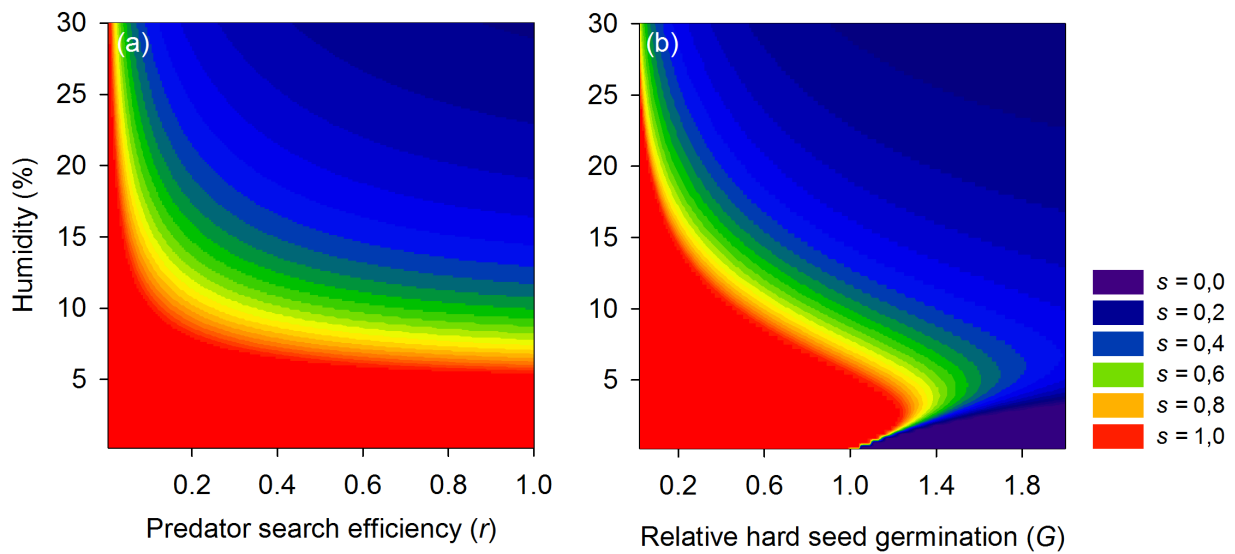
Figure S1. Optimal plant strategies.

Figure S1. Optimal plant strategies. Predicted fractions of hard and soft seeds produced by plants at different environmental humidity (*h%*) as a function of a) predator search efficiency (*r*) and b) the survivability of hard seeds relative to soft seeds in a cache (*G*). In a) the two seed morphs have the same relative seed germination (*G* = 1.0) and in b) predator search efficiency (*r*) = 0.7, other parameters as in table 1. Soft:hard seed proportions increase from blue to red (*s* = 0 pure hard seed strategy; *s* = 1 pure soft seed strategy).