

Assessing the benefits of frugivory for seed germination: the importance of the deinhibition effect

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Summary

1. Many studies have examined the effects of frugivores on the germination of seeds of fleshy fruited plants. However, three key issues are rarely addressed: the need to measure germination of seeds in intact fruits; the effect of germination conditions on results; and the distinction between dead *vs* dormant seeds.

2. A literature review including 51 plant species from 28 families found that the often-measured scarification effect (germination of bird-defecated *vs* hand-cleaned seeds) is significantly smaller than the rarely-measured deinhibition effect (germination of hand-cleaned seeds *vs* those in intact fruits).

3. Both the literature review and new experimental data show that germination conditions affect germination. In particular, seeds in intact fruits have much lower germination percentages in Petri dishes than in the field. Poor germination from intact fruits in Petri dishes may be an artefact.

4. A field experiment with three New Zealand species showed variable effects of non-removal of the fruit pericarp. The retention of the pericarp had no effect on germination in *Nestegis cunninghamii*; increased the proportion of seeds entering dormancy in *Melicytus lanceolatus*; and greatly increased seed mortality in *Pennantia corymbosa*.

5. Germination experiments must be designed carefully to evaluate accurately the risks for plants of frugivory mutualism failures.

Key-words: fruit, germination experiment, germination inhibitors, gut passage, vertebrate seed dispersal

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Introduction

Vertebrate–fruit mutualisms can result in benefits to the plant, not only from the movement of seeds away from the parent (Schupp 1993; Willson & Traveset 2000), but also from changes to germination caused by the passage of a seed through the digestive tract of a vertebrate such as a bird (Krefting & Roe 1949; Rick & Bowman 1961; Ketring 1973; Van der Pijl 1982). These germination effects have been studied extensively. Frugivores can affect seed germination directly in three ways: (1) through scarification of the seed coat, which increases the permeability of the coat to water and gases (scarification effect); (2) through removal of germination inhibitors by separation of the seeds from the pulp (deinhibition effect); and (3) through enhancement of germination and seedling growth from faecal material surrounding the seed (fertilization effect) (Traveset & Verdú 2002).

However, two recent papers argue that much of the literature tests germination effects incompletely, or in

ways that may introduce unintended effects (Kelly, Ladley & Robertson 2004; Samuels & Levey 2005). In this paper we present data to back up those arguments on three key points: first, the need to measure the germination of seeds in intact fruits; second, the need to conduct such experiments in the field; and third, the need to discriminate between dead and dormant seeds at the end of trials.

The first key point is the need to compare germination of bird-dispersed seeds with that of seeds in intact fruits. Many studies have evaluated the germination benefit of dispersal by birds and other dispersal agents (Traveset 1998; Traveset & Verdú 2002). The majority of these studies test the scarification effect, by comparing the germinability of seeds that have passed through the gut of a vertebrate, with seeds that have been hand-cleaned (Samuels & Levey 2005). The difference in germination is generally interpreted as the benefit of gut passage, hence the dependence on vertebrates for germination enhancement. Traveset's (1998) review, which included 183 plant species in 68 families, showed that scarification effects were small and inconsistent. Sixteen per cent of studies found that scarification had

a negative effect on the percentage of seeds that germinated, while 36% found positive effects.

However, studies of this scarification effect do not allow us to predict what might happen if birds stopped feeding on the fruit, as the critical need is to compare cleaned seeds with seeds that are left intact in the fruit – such as happens when fruits are not dispersed, but fall to the ground whole (Kelly *et al.* 2004). The removal of inhibitors found in the pulp of fruits (deinhibition effect) is a second result of gut passage, but is not measured in studies designed to measure scarification. The sum of the scarification, deinhibition and fertilization effects represents the total germination effect of gut passage (Samuels & Levey 2005). Only 22% of studies reviewed by Samuels & Levey (2005) included intact fruits as a control treatment, and were thereby able to measure the size of the deinhibition effect. There has, to date, been no formal comparison of the relative effect sizes of the scarification effect and the deinhibition effect, although some examples from New Zealand and elsewhere suggest that the deinhibition effect may be large (Wenny 2000; Kelly *et al.* 2004). Here we present a review of published effect sizes for the scarification and deinhibition effects.

The second point is to consider the conditions under which germination trials are conducted: this appears to be especially important for seeds in intact fruits. Previous tests have been conducted mostly in the laboratory or glasshouse, rather than under field conditions (Burrows 1997; Traveset 1998; Traveset & Verdú 2002), despite the fact that germination studies show varied results under different environmental conditions (Yagihashi, Hayashida & Miyamoto 1999; Traveset & Verdú 2002). The conditions used can affect germination by altering the ability of inhibitors to leach away, and by altering the micro-organisms available for decomposition, affecting fruit wall and pulp breakdown (Burrows 1997; Morpeth & Hall 2000). All these alterations may have a larger effect on intact fruits than on other treatments. Only a few studies have compared field and laboratory conditions (Traveset & Verdú 2002), and they have found, variously, a greater effect of treatments in the laboratory (Bustamante, Simonetti, & Mella 1992; Bustamante *et al.* 1993; de Figueiredo & Perin 1995; Yagihashi, Hayashida & Miyamoto 1998); little difference between conditions (Myers 1984; de Figueiredo & Perin 1995; de Figueiredo & Longatti 1997); or a greater effect in the field (Traveset, Riera & Mas 2001). Here we show that the conditions used for trials with intact fruits have a very large effect on the results of the trials.

Our third key point concerns the fate of seeds that have not germinated by the end of the trial. The majority of seed germination studies extended for only a few months, which may not be long enough to allow for full germination of dormant but viable seed (Burrows 1997; Traveset 1998). To take an extreme example, seeds of the New Zealand canopy tree species *Prumnopitys ferruginea* may continue to germinate more than

4 years after dispersal (Beveridge & Smale 1981; Clout & Tilley 1992). In certain species a delay in germination caused by inhibitors in the pericarp may be beneficial, by allowing for dispersal in time rather than in space (Kelly *et al.* 2004). A key question is to know whether non-germinated seeds at the end of the experiment are dead or dormant, and also to determine whether the balance between these two outcomes is affected by the environmental conditions of the trial (Kelly *et al.* 2004).

For all these reasons, despite a very extensive literature on germination trials, we know very little about the likely consequences in the field of dispersal failure for most of the tested plant species worldwide (Samuels & Levey 2005). The goals of this study were to: (1) review the relative effect sizes of the scarification and deinhibition effects; (2) compare the effects of germination conditions on germination percentages, both in the literature review and within three New Zealand plant species; and (3) present a seed germination trial that more appropriately estimates the vulnerability of fruit-bearing species to dispersal failure, illustrated with data for three species from the New Zealand flora.

Throughout this paper we concentrate largely on final germination percentages. Previous studies have measured both the final germination percentage and the speed of germination (Traveset 1998), both often confusingly called germination 'rates'. We avoid the use of the term 'rate' as potentially confusing, and recommend that others discriminate clearly between final germination percentage and germination speed. We do not present analysis of the speed of germination, because we believe the timing of germination may vary in the field *vs* the laboratory, and earlier germination is not always better. For example, in three species of (dry-fruited) herbs, Kelly (1989) showed that, within a season, early-germinated seedlings in the field did better than average in *Euphrasia pseudokernerii*, but worse than average in *Linum catharticum* and *Gentianella amarella*. Moreover, delayed germination from seeds in intact fruits may represent a conditional strategy within a species to have some seeds disperse in space while others disperse in time (Kelly *et al.* 2004). Therefore we do not discuss germination speed further in this paper.

Materials and methods

EFFECT SIZES

To review the relative magnitudes of the scarification effect and the deinhibition effect, we adapted the methods of Traveset & Verdú (2002). We searched the literature for germination studies of fleshy fruited plants that included all three treatments recommended by Samuels & Levey (2005): defecated by a bird; cleaned by hand; and in intact fruits. We restricted our review to bird dispersers, as these were the most-studied group of animal dispersers, and other animals may have different gut morphologies and scarification effects

(Traveset 1998). We found data for 51 bird-dispersed plant species from 44 genera in 28 different plant families (Appendix 1), from recent reviews (Traveset & Verdú 2002; Samuels & Levey 2005) and the primary literature (Cowling *et al.* 1997; Panetta & McKee 1997; Penner, Moodie & Staniforth 1999; Figueroa & Castro 2002; Paulsen & Högstedt 2002). The effect sizes were measured using odds ratios (ORs) following Traveset & Verdú (2002). The effect size for scarification was $\ln(\text{defecated OR}/\text{hand-cleaned OR})$, and for deinhibition was $\ln(\text{hand-cleaned OR}/\text{intact fruits OR})$. Where a particular treatment had 0 or 100% germination, the log odds ratio is infinite, so we added/subtracted 0.5 (where counts of the numbers of seeds were available) or 0.05% (where only the percentages of germination were available). This means our average effect sizes are conservative estimates.

In some cases there were data for a single plant species for seeds defecated by several different species of bird, or several different sets of intact or hand-cleaned

trials (e.g. from different germination conditions or different authors). From the 51 species, this gave 74 different estimates of the scarification effect, and 56 estimates of the deinhibition effect. We compared these with a one-way ANOVA to see if the mean effect sizes were different across all data sets. To correct for the partial non-independence in that analysis, we also calculated a single mean effect size for the scarification and deinhibition effects for each plant species (using the arithmetic mean of multiple effect-size estimates), giving a paired data set with 51 cases, which was tested with a paired *t*-test.

GERMINATION CONDITIONS

To test the effect of germination conditions on germination percentages, we classified the studies reviewed above by the conditions used for their germination trials (laboratory, glasshouse or field). One-way ANOVAs were used to test for variation among these three sets of conditions in the effect sizes for the scarification and deinhibition effects.

Because those ANOVAs largely used different plant species in the different conditions, we ran experiments comparing different conditions within single species. Burrows (1996a, 1996b, 1996c, 1997, 1999) ran trials on many different New Zealand plant species, and most had low or zero germination from intact fruits in Petri dishes (Kelly *et al.* 2004). To compare Burrows's results from Petri dishes with data from field and glasshouse conditions, we selected three large-fruited species from different plant families for which fruiting material was obtainable: *Corynocarpus laevigatus* J.R. et G. Forst. (Corynocarpaceae, mean fruit length \times width 33 \times 18 mm); *Beilschmiedia tawa* (A. Cunn.) Benth. et Hook. f. ex Kirk (Lauraceae, 28 \times 19 mm); and *Ripogonum scandens* J.R. et G. Forst. (Smilacaceae, 12 \times 11 mm). All three species are bird-dispersed (Clout & Hay 1989). For field and glasshouse trials with *C. laevigatus*, we used a site near Kaikoura (42°15' S, 173°48' E, elevation 20 m a.s.l.). For *B. tawa* we used 2 year's data at each of two sites, Blue Duck (42°14' S, 173°47' E, 420 m a.s.l.) and Pelorus (41°17' S, 173°34' E, 60 m a.s.l.). For *R. scandens* the glasshouse trial used seeds from Blue Duck, and the field trial was at Tiritea (40°25' S, 175°39' E, 250 m a.s.l.). For all three species fresh, intact fruits were collected in the field. For the field trials, seeds in intact fruits and hand-cleaned seeds were immediately placed in a randomized array of short lengths of open-ended alkathene pipes pushed into the forest litter layer at the site where the seeds were collected (Fig. 1). The pipes were covered with a 5.8-mm mesh cage to keep out all vertebrate predators. The percentage of seeds germinated was recorded by noting seedling emergence every 1–2 months until all seeds had either germinated or rotted. For the glasshouse trials, intact fruits and hand-cleaned seeds were placed on potting mix then covered with leaf litter from the Blue Duck site, and kept in an unheated



Fig. 1. Experimental set-up for field-germination trials. Seeds from individual fruits were placed in a randomized array of short lengths of open-ended alkathene pipes pushed partly into the forest litter and covered with a mesh cage to keep out vertebrate predators. Germination was recorded every 1–2 months by visual inspection of each seed.

glasshouse at the University of Canterbury, the same location as used by Burrows (1996a, 1996b, 1999). We tested the effects of species, condition (Petri dishes, potting mix or field) and treatment (intact fruit vs hand-cleaned) on final germination percentages using a binomial GLM run in s-PLUS ver. 4.5 (MathSoft Inc.).

GERMINATION TRIALS

To measure deinhibition effects on germination and dormancy under field conditions, we compared the germination of hand-cleaned seeds with seeds in intact fruits of another three New Zealand tree species: *Nestegis cunninghamii* (Hook. f.) L.A.S. Johnson (Oleaceae); *Pennantia corymbosa* J.R. Forst & G. Forst. (Icacinaceae); and *Melicytus lanceolatus* Hook. f. (Violaceae). These species were chosen because they come from three different families with different fruit structures, and fruiting material for all three was available at a single site. *Nestegis cunninghamii* is a canopy tree that produces orange or red single-seeded drupes averaging 19×9.6 mm. *Pennantia corymbosa* is a canopy tree that makes clusters of small, single-seeded drupes 7×4.3 mm. *Melicytus lanceolatus* is a small tree or shrub that produces small berries 6×5.1 mm containing four to seven seeds. All are commonly bird-dispersed (Clout & Hay 1989; Burrows 1995, 1996c). Bird-defecated seeds were not included in these trials because the study was designed to measure the deinhibition effect.

Ripe fruits were collected from several trees of each species, and stored for up to a week at 4 °C in plastic bags before hand-removal of the pericarp (where appropriate), and sowing. Seeds were placed in alkathene pipes as described above, in podocarp–broadleaf (mixed evergreen conifer/angiosperm) forest, Ohakune in the central North Island, New Zealand (39°22.8' S, 175°25.9' E, 740 m a.s.l.), near where the fruits had been collected. The pipes were covered with 9-mm mesh which excluded all vertebrate predators except mice (*Mus musculus*). Ship rats (*Rattus rattus*) and mice are both important seed predators in New Zealand forests (Fitzgerald *et al.* 1996; Williams *et al.* 2000; Alley *et al.* 2001; Wilson *et al.* 2003; Ruscoe *et al.* 2004), but in forests like our study site, ship rats are more common (King *et al.* 1996). We saw no evidence of mouse predation in our study. Seedling emergence was recorded every 1–2 months for a total of 27 months.

All the tubes were checked for intact seeds at the end of 27 months by removing the soil and sieving, and recovered seeds were given the opportunity to germinate on damp paper pads in plastic dishes in growth chambers at 20 °C with 12 h daylength. Those seeds that did not germinate were tested with tetrazolium trichloride to determine if they were still viable. Thus seeds had one of three fates at the end of this experiment: (1) germinated within 27 months; (2) not germinated but still viable after 27 months (dormant and potentially able to germinate later); or (3) dead, doubtfully viable or not

recovered after 27 months. As the tubes constrained seeds spatially, 'not recovered' seeds had probably decomposed. The proportions of seeds from hand-cleaned vs intact fruits that germinated during the study or remained viable at the end of the study were compared for each species using χ^2 tests.

Results

EFFECT SIZES

Across the 51 plant species, the scarification effect was usually small (mean = 0.85 ln OR, and 70% of the 74 cases were within ± 1 of zero, the point at which germination is identical for defecated and hand-cleaned seeds; Fig. 2). In contrast, deinhibition effects were much larger (mean = 4.23 ln OR, with only 23% of the 56 cases within ± 1 of zero), significantly so across all data according to a one-way ANOVA ($F_{1,128} = 44.9$, $P < 0.0001$). When using species means of the scarification and deinhibition effects for each of the 51 species, the same conclusion was reached (paired *t*-test, means 0.39 and 4.45, respectively, $t = -7.03$, $df = 50$, $P <$

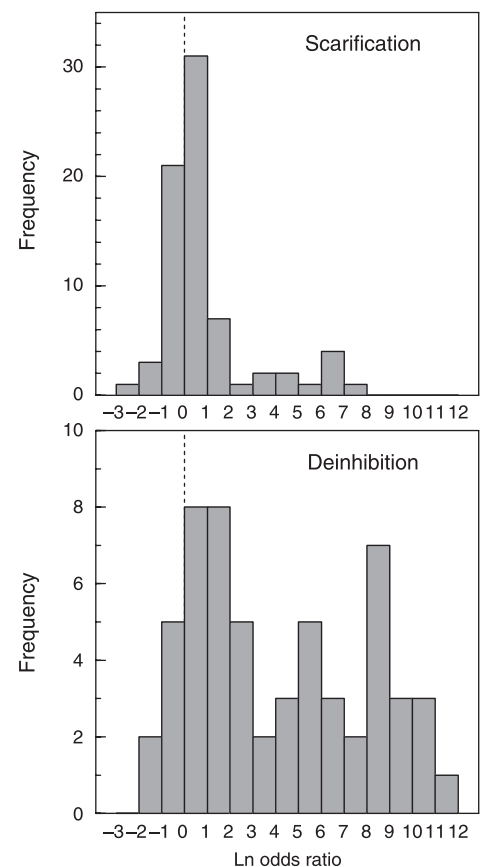


Fig. 2. Germination effect sizes (natural log of the odds ratio) from the literature for the scarification effect (gut passage/hand-cleaned) and the deinhibition effect (hand-cleaned/intact fruits) for 51 plant species, some with multiple dispersers or germination conditions. The dotted line at $x = 0$ shows no effect; to the right of this shows enhancement of germination. $N = 74$ cases for scarification and 56 cases for deinhibition.

0.0001). In only seven of the 51 species was the scarification effect larger than the deinhibition effect.

GERMINATION CONDITIONS

The conditions used for germination trials from our literature review had significant effects on both the scarification effect and the deinhibition effect (Table 1). For the scarification effect, larger effect sizes were found in the glasshouse than in laboratory or field conditions. For the deinhibition effect, very large effect sizes were found in laboratory studies relative to effects in the field or glasshouse, mainly because laboratory trials often reported zero germination from intact fruits, whereas this was less common in field or glasshouse conditions.

The germination results for *C. laevigatus*, *B. tawa* and *R. scandens* under all three conditions showed the same patterns (Fig. 3). Germination percentages were high in all conditions for hand-cleaned seeds. Germination of seeds from intact fruits was generally slightly lower than for hand-cleaned seeds in the field, and in pots in the glasshouse, but germination from intact fruits in Petri dishes was zero for all three species. A binomial GLM showed that there were significant effects of species, treatment, and the condition \times treatment interaction (Table 2). In other words, the effect of condition varied between the two treatments, consistent with the conclusions from the literature review.

GERMINATION TRIALS

Hand-cleaning the pericarp from *N. cunninghamii* seeds had no significant effect on percentage germination

Table 1. Effect of germination conditions (laboratory, glasshouse or field) on measured effect sizes for the scarification effect (gut passage vs hand-cleaned) and the deinhibition effect (hand-cleaned vs intact fruits) for germination data on 51 plant species. The response variable is the natural log of the odds ratio (see text)

(a) Mean effect size

Condition	Scarification		Deinhibition	
	N	Mean ln OR	N	Mean ln OR
Field	19	0.2763	13	1.7831
Glasshouse	18	2.7522	6	1.0683
Laboratory	37	0.2154	37	5.5959

(b) One-way ANOVA

Source	df	SS	MS	F	P
Scarification effect by condition					
Condition	2	86.285	43.1426	12.8	< 0.0001
Error	71	240.042	3.3809		
Total	73	326.328			
Deinhibition effect by condition					
Condition	2	206.847	103.424	10.9	0.0001
Error	53	504.213	9.513		
Total	55	711.060			

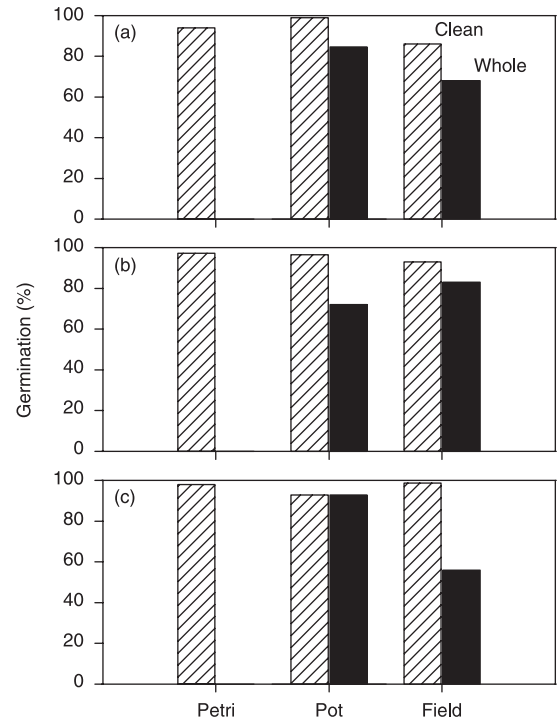


Fig. 3. Effect of germination conditions (Petri dishes, pots in glasshouse, or field) and treatment [hand-cleaned (shaded bars) vs intact fruits (solid bars)] on seed germination percentage for three fleshy fruited New Zealand species. (a) *Corynocarpus laevigatus*; (b) *Beilschmiedia tawa*; (c) *Ripogonum scandens*. Germination was zero for all seeds in intact fruits in Petri dishes.

(Fig. 4; $\chi^2 = 0.72$, $df = 1$, $P = 0.397$). More than half the seeds in both treatments germinated before the end of the 27-month study.

In contrast, removal of the pericarp was necessary for good germination of *P. corymbosa* and *M. lanceolatus* under field conditions. *Pennantia corymbosa* seeds that were not cleaned mostly died within 24 months, while hand-cleaned seeds mostly germinated (Fig. 4; $\chi^2 = 112.24$, $df = 1$, $P < 0.001$). Similarly, hand-cleaning had a significant effect on the fate of *M. lanceolatus* seed, mostly due to the boost of germination in cleaned seed. Little uncleaned seed germinated in the first 24 months, and some of the *M. lanceolatus* seed remained dormant in both treatments ($\chi^2 = 9.81$, $df = 2$, $P = 0.007$).

Thus the three species covered the three major possible outcomes from this experiment. In *N. cunninghamii*, seeds in intact fruits mostly germinated; in *P. corymbosa* they mostly died; while in *M. lanceolatus* seeds in intact fruits were more likely to enter extended dormancy.

Discussion

Our data show that the methodological concerns raised in recent papers (Kelly *et al.* 2004; Samuels & Levey 2005) are valid. Until now, a majority of papers studying the impact of frugivores on seed germination

Table 2. Analysis of deviance on effects of germination conditions (Petri dishes, pots in glasshouse, or field) and treatment (hand-cleaned vs intact fruits) on final germination percentage for *Corynocarpus laevigatus*, *Beilschmiedia tawa* and *Ripogonum scandens*

Model	df	Deviance	Residual df	Residual deviance	F	P
Null	26	771.7685				
Species	2	101.3484	24	670.4201	4.73	0.0215
Condition	2	15.7177	22	654.7024	0.73	0.4933
Treatment	1	260.5724	21	394.1300	24.32	0.0001
Condition × treatment	2	162.4228	19	231.7072	7.58	0.0034

The analysis used a GLM with binomial error distribution and logit link function. The significant condition–treatment interaction shows that the effect of condition varies between the two treatments.

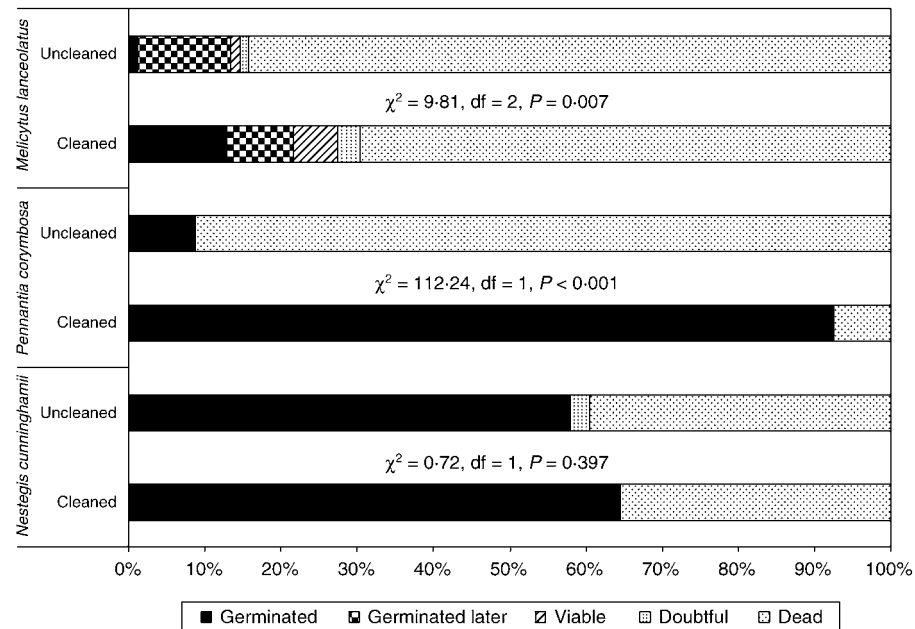


Fig. 4. Fate of hand-cleaned seeds and seeds in intact fruits of three fleshy fruited New Zealand species in the field. The proportion of seeds falling into three fates was tested with χ^2 tests: (i) germinated in the field ('germinated'); (ii) recovered alive after 27 months ('germinated later' or tested 'viable'); or (iii) not recovered, doubtfully viable or unviable, or empty ('doubtful' and 'dead').

have failed to measure germination in intact fruits, have often used germination conditions where leaching and microbial activity differ from the natural environment, and give little or no idea of how many seeds enter dormancy rather than dying. All this means it is difficult to assess the true effect of frugivores on germination percentages, or to assess the likely impact on plant reproduction if frugivores should fail to consume fruits.

Of course, some studies may have more narrowly defined objectives, for which current methods are adequate (Samuels & Levey 2005), such as comparing the scarification effect among different frugivores. The scarification effect may be particularly important among non-volant frugivores which grind their food thoroughly; our conclusion that the deinhibition effect is larger than the scarification effect is based only on birds. However, we support the call of Samuels &

Levey (2005) for more carefully designed experiments, and more explicitly described aims, in papers on the effects of frugivory on germination.

Also, by presenting here experiments that show the importance of the deinhibition effect, we do not mean that researchers should ignore the scarification effect. Both effects are important (although the deinhibition effect was usually larger). However, the two treatments that occur naturally are bird-dispersed seeds and seeds in intact fruits, so both would be included in the ideal study. Nevertheless, the hand-cleaned treatment does have two advantages. First, in conjunction with bird-dispersed and intact treatments, hand-cleaning provides information about the mechanism for any overall effect of gut passage. Second, hand-cleaned seeds have experimental advantages, being easy to produce and able to be applied as a randomized treatment. In contrast, bird-processed seeds are often only available

opportunistically, may be of unknown age, and may have arisen by non-random selection from the fruits on offer. Therefore, ideally, a study would include bird-dispersed, hand-cleaned and intact-fruit treatments (Samuels & Levey 2005).

Such a study can evaluate the scarification and deinhibition effects, but not the fertilization effect, which is harder to incorporate realistically in a study. The strength of the fertilization effect probably varies even among different bird droppings, according to factors such as the bird species, the recent diet of the individual bird, whether the dropping becomes physically scattered on impact or remains in one lump, and how much rainfall occurs immediately after deposition. Further study of the fertilization effect that evaluates the extent of such variation would be very valuable.

Perhaps the most important message of this paper is that the three key factors we identify interact with each other. Like earlier papers, we argue that it is important to include seeds in intact fruits as one of the treatments when measuring germination. Second, the conditions used for germination can affect the measured germination percentages; it appears that this effect is especially pronounced for intact-fruit treatments. Given that conditions affect the results, it is preferable to use natural (field) conditions so that the results are applicable to the real world (Vander Kloet & Hill 2000). Third, we argue for the importance of discriminating between dead and dormant seeds at the end of any experiment, as dormancy induced by a treatment may represent not a cost to the plant so much as a conditional strategy (Kelly *et al.* 2004). It is possible, although we know of no data to test this, that the percentage of seeds moving into dormancy vs dying may also be affected by germination conditions. Certainly, varied germination conditions in the papers we reviewed were reported to be associated with differences in fungal growth, and changes in the microflora can strongly affect final germination percentages (Morpeth & Hall 2000). Microorganisms might affect dormancy and mortality of seeds as well as germination. Hence dormancy is most usefully measured on seeds, including seeds in intact fruits, kept under field conditions.

Our third experiment was designed to illustrate all these points. This study showed that the deinhibition effect may vary among plant species. The removal of the pericarp had no effect in the field on seed germination in one species (*N. cunninghamii*); altered the proportion of seeds that entered dormancy in a second species (*M. lanceolatus*); and greatly increased germination of a third species (*P. corymbosa*). Future studies will help to determine which of these three possible outcomes is most common in fleshy fruited plants in general.

Because germination percentages may vary considerably depending on environmental conditions (Traveset & Verdú 2002), studies carried out under field conditions are necessary to clarify what will happen in the field if bird dispersers are no longer available. Our study

suggests that a change in the fruit-dispersing fauna may have important and variable effects on plant recruitment and forest composition. Although there is little evidence of inadequate dispersal in New Zealand plants (Kelly *et al.* 2004), two lines of evidence can help predict which plant species are most vulnerable to the disruption of mutualism. First, large-fruited species such as *B. tawa* and *C. laevigatus* that are dependent on only one or a few species of disperser may be particularly vulnerable (Clout & Hay 1989; Burrows 1994; Kelly *et al.* 2004). Second, plant species whose seeds cannot germinate if retained within the fruits are more dependent on birds for dispersal and effective recruitment. However, measurements under field conditions of germination percentages from intact fruits are needed to estimate accurately the risk of reproductive failure in plants.

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Appendix 1. Data sources and plant species included in the analysis of effect sizes

Barnea, Yomtov & Friedman (1991) (*Arum hygrophilum*, *Asparagus aphyllus*, *Ephedra campylopoda*, *Myrtus communis*, *Rhamnus alaternus*, *Rhamnus palaestinus*, *Rubia tenuifolia*); Clergeau (1992) (*Rubus fruticosus*, *Sambucus nigra*, *Solanum nigrum*); Cowling *et al.* (1997) (*Euclea racemosa*, *Sideroxylon inerme*); Debussche (1985) (*Asparagus acutifolius*, *Hedera helix*, *Pyracantha coccinea*); de Figueiredo *et al.* (1995) (*Ficus microcarpa*); Figueroa & Castro (2002) (*Gaultheria mucronata*, *Luma apiculata*, *Myrceugenis planipes*); Fukui (1995) (*Aucuba japonica*, *Callicarpa dichtoma*, *Celastrus orbiculatus*, *Cornus florida*, *Daphniphyllum macropodum*,

Eurya japonica, *Fatsia japonica*, *Idesia polycarpa*, *Ilex crenata*, *Ilex serrata*, *Ligustrum obtusifolium*, *Morus bombycis*, *Ophiopogon japonicus*, *Parthenocissus tricuspidata*, *Phytolacca americana*, *Pourthiaea villosa*, *Pyracantha coccinea*, *Viburnum dilatatum*); Izhaki & Safriel (1990) (*Osyris alba*, *Pistacia palaestina*, *Rhamnus palaestinus*, *Smilax aspera*); Ladley & Kelly (1996) (*Alepis flavida*, *Ileostylus micranthus*, *Peraxilla colensoi*, *Tupeia antarctica*); Lisci & Pacini (1994) (*Ficus carica*); McDiarmid, Ricklets & Fosters (1977) (*Stemmadenia donnell-smithii*); Panetta & McKee (1997) (*Schinus terebinthifolius*); Paulsen & Högstedt (2002) (*Sorbus aucuparia*); Penner *et al.* (1999) (*Toxicodendron radicans*); Yagihashi *et al.* (1998) (*Sorbus commixta*); Yagihashi *et al.* (1999) (*Prunus sargentii*, *Prunus ssiori*).