



# On the need to evaluate costs and benefits of synzoochory for plant populations

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## Funding information

Narodowe Centrum Nauki, Grant/Award Number: 2015/17/N/NZ8/01565 and 2018/30/M/NZ8/00052

Handling Editor: Richard Shefferson

## Abstract

1. Many species interactions occur along a continuum from mutualistic to antagonistic. Among these interactions, the effects of seed-dispersing granivores (synzoochory) are especially interesting because the benefits and costs are so striking.
2. Here, we respond to a commentary by C. M. Moore and J. W. Dittel ('On mutualism, models, and masting: the effects of seed-dispersing animals on the plants they disperse'). We focus on the points that were most thought-provoking to us, specifically the notions that (a) synzoochory is widespread, and therefore ought to be beneficial for plants, (b) dispersal should reduce negative density dependence and (c) plant life spans are at least an order of magnitude longer than typical study lengths.
3. We argue that (a) widespread occurrence of an interaction cannot serve as an argument that this interaction is mutualistic, (b) dispersal effects on density dependence are variable and need to be tested for every particular species pair and (c) Short-term studies can be used to gain mechanistic understanding of interactions even without risky long-term extrapolations.
4. *Synthesis*. Evaluating the costs and benefits of synzoochory for plant populations under different ecological contexts will help to understand the ecological principles of the interaction but also allows to move the interaction towards each end of the antagonism–mutualism continuum in nature management and conservation.

## KEYWORDS

conditional mutualism, context dependency, masting, scatter-hoarding, seed caching, seed dispersal

## 1 | INTRODUCTION

Many species interactions occur along a continuum from mutualistic to antagonistic. Among these interactions, the effects of seed dispersal by granivores (synzoochory) are especially interesting because the benefits and costs are so striking. The primary cost is seed predation, and its many possible benefits have been outlined by Moore and Dittel (2020); see also (Gómez, Schupp, & Jordano, 2019; Pesendorfer, Sillett, Koenig, & Morrison, 2016). We are pleased that Moore and Dittel found our recent article (Bogdziewicz, Crone, & Zwolak, 2020)

thought-provoking enough to motivate further development (Moore & Dittel, 2020). Here, we focus on the points in their commentary that were most thought-provoking to us. We hope that making these points more explicit will inspire further discussion, not only between our research teams but also among the community of scholars interested in plant–granivore interactions (e.g. Aliyu, Thia, Moltchanova, Forget, & Chapman, 2018; Beckman et al., 2020; Brehm, Mortelliti, Maynard, & Zydlewski, 2019; Cao, Yan, & Wang, 2018; Jácome-Flores, Jordano, Delibes, & Fedriani, 2020; Rehm, Fricke, Bender, Savidge, & Rogers, 2019; Yang, Yan, Gu, & Zhang, 2020).

**Response to:** Moore and Dittel 'On mutualism, models, and masting: the effects of seed-dispersing animals on the plants they disperse'.

At the most basic level, we agree with Moore and Dittel. We all seem convinced that the dynamics of costs and benefits in plant–scatterhoarder interactions deserve close attention. However, we probably differ in our baseline assumptions. Moore and Dittel appear to assume that the interaction is most likely mutualistic. They state that they *observe* mutualistic character of this interaction in nature. Thus, they search for reasons why conclusions of our paper (that the investigated interaction was antagonistic over the period of our study) are in disagreement with their observations. In contrast, we think that more rigorous tests would be needed to conclude that scatter-hoarding is nearly always positive, even when we refer to positive as mutualistic in the long run. We are also convinced that testing for mutualistic versus antagonistic interaction outcome is valuable even without extrapolating beyond the time-frame of the study. Below, we discuss these notions in more detail.

## 2 | WIDESPREAD OCCURRENCE OF SYNZOOCHORY AMONG PLANT TAXA

Moore and Dittel (2020) assert that synzoochory is widespread among plant taxa and associated with higher rates of speciation, which means that it is beneficial for plants, at least over evolutionary timeframe. This idea is intuitively appealing, and we have in the past expressed it ourselves (e.g. Bogdziewicz, Crone, et al., 2020, 1st paragraph of introduction). However, upon reflection, we realize that this argument cannot be used to infer that a given interaction is mutualistic. There are at least three reasons why we cannot assume synzoochorous relationships are mutualistic, simply because they are widespread.

First, the widespread existence of a trait does not necessarily imply it is beneficial, even if it increases speciation rates. For example, nearly all taxa across the tree of life are subject to some forms of disease, and in at least some cases disease is associated with speciation (Schulze-Lefert & Panstruga, 2011). However, this pattern does not mean that host–disease relationships are generally mutualistic.

Second, synzoochory is a diffuse interaction, which means that seeds of a given plant species are typically eaten and dispersed by many different animal species (Gómez et al., 2019). Even if synzoochory is on average beneficial across animal communities, it could still be that some animal taxa are mutualists, whereas others are net antagonists (e.g. corvids vs. small mammals in Gómez et al., 2019, their fig. 1). Testing the notion that a particular plant–granivore pair is mutualistic is not trivial, even if the outcome at a community level is known to be positive. Similarly, even if interactions are positive in the long term, they can switch between mutualism and antagonism with ecological conditions. Investigating this switching enables us to understand properties of the studied systems.

Finally, it is clear that environmental conditions have changed rapidly during the late 20th and early 21st century, due to, for example, changing temperature, precipitation, species introductions, overharvesting and habitat fragmentation (McConkey et al., 2012). Even if plant–granivore interactions were mutualistic during most of

the 20th century and prior eras, it is not obvious that they would remain mutualistic under current conditions.

## 3 | DISPERSAL (OFTEN) REDUCES NEGATIVE DENSITY DEPENDENCE

Zwolak and Crone (2012) provided a simple model of costs and benefits in plant–scatterhoarder interactions that is readily expanded by adding more modules. The original model included only effects of seed burial and consumption. Its modified version (Bogdziewicz, Crone, et al., 2020) incorporated the effects of seed pilferage. Moore and Dittel (2020) further extended our model by adding a negative density-dependent effect that occurs when seeds are not dispersed by granivores. We appreciate this expansion and are excited about Moore and Dittel's interest in learning about plant–granivore systems via combining models and data. In many plants, especially trees, conspecific seed and seedling densities are higher under parent plants, which means that dispersal can effectively reduce intraspecific competition. Inclusion of density- and distance-dependent (DDD) effects is certainly valuable because DDD is pervasive and plays an important role in structuring plant communities worldwide (Hille Ris Lambers, Clark, & Beckage, 2002; Johnson, Beaulieu, Bever, & Clay, 2012; Putten et al., 2013). Moore and Dittel (2020) assert that incorporation of DDD will shift the interaction towards mutualism. This might often be true. However, we would like to make a cautionary note that in other cases, the effect DDD might be null or even negative. There are two reasons why this might happen.

First, benefits of seed transportation are often, but not always seen in synzoochorous and endozoochorous interactions (Fricke et al., 2013; Hirsch, Kays, Pereira, & Jansen, 2012). In the study that prompted this discussion (Bogdziewicz, Crone, et al., 2020), we directly tested for benefits of seed transportation by planting seeds at distances from 0 to 25 m from their parent plants. In one oak tree species (*Quercus petraea*), we found no effect of planting distance on seedling establishment. In another oak species (*Quercus rubra*), we found negative effects of planting distance on establishment. Of course, it is possible that benefits of dispersal would appear later in life, as suggested by Moore and Dittel (2020). However, when others have looked for distance-dependent benefits of dispersal on oak seedling survival and growth, they often did not find any (Comita et al., 2014; Reinhart, Johnson, & Clay, 2012) or the effects were complex and species specific (Wróbel, Crone, & Zwolak, 2019). Similarly, with other plants, many show such effects, but many do not (e.g. Svenning, Fabbro, & Wright, 2008, Anderson, 2009; see also fig. 4 in meta-analysis by Comita et al., 2014). The lack of benefits associated with dispersal away from maternal plants appears linked to commonness, with abundant species less likely to exhibit negative DDD than rare ones (Comita, Muller-Landau, Aguilar, & Hubbell, 2010; Johnson et al., 2012; Mangan et al., 2010). At any rate, it may be that positive effects of dispersal occur in the majority of zoochorous plant species. However, for any particular species pair, the effects of

dispersal on seedling establishment and survival are not clear in the absence of experiments.

Second, dispersal of seeds by animals can itself generate negative density dependence, therefore reducing the benefits of dispersal. This phenomenon attracted considerable attention in frugivore systems, where seeds are often deposited together in latrines, under roosts, sleeping sites, fruiting trees, etc. This can generate intense intraspecific (Spiegel & Nathan, 2010) or heterospecific competition ('contagious dispersal': Clark, Poulsen, Connor, & Parker, 2004; Kwit, Levey, & Greenberg, 2004; Razafindratsima & Dunham, 2016; Wright, Calderón, Hernández, Detto, & Jansen, 2016). Similar effects can be expected in synzoochorous systems because scatterhoarders often put several seeds in one cache (Vander Wall, 1990). Thus, density dependence terms might actually appear on both sides of the equation. In the example below,  $\delta_M$  denotes density dependence near the mother plant, experienced by undispersed seeds, and  $\delta_A$  stands for density dependence after dispersal by animals (scatterhoarders):

$$e_S \delta_M < p_H p_C e_C \delta_D + (1 - p_H) e_S \delta_M.$$

In this case, it is again important to quantify the relative strengths of costs and benefits to determine the net outcome.

#### 4 | EXTRAPOLATING FROM SHORT-TERM STUDIES

Moore and Dittel (2020) argue that it is 'incorrect to assume the overall interaction from a temporally limited sample'. We agree. In fact, we emphasized in our paper that the investigated interaction was antagonistic 'during the period of the study'. There is an important distinction between trying to determine the outcome of an interaction over evolutionary time (averaged over many generations), versus over lifetime of an organism (averaged over changing ecological conditions), versus in a given year (measured during specific circumstances). All have different objectives and present different challenges. In Bogdziewicz, Crone, et al. (2020), we focused on the latter. Our goal was not to extrapolate to the longer time-scales, but rather to gain more mechanistic understanding of the dynamics of costs and benefits in the studied interaction. We found that during that year, costs of consumption were high relative to the benefits of seed caching and the effects of seed transportation away from adult plants were null, rendering the interaction antagonistic. Counterintuitively, acorns faced better prospects without interactions with rodents.

Moore and Dittel (2020) further added that 'masting may in fact be the reason the interaction can be mutualistic'. We agree that mast years (synchronous production of large seed crops: Bogdziewicz, Ascoli, et al., 2020; Kelly & Sork, 2002; Pearse, Koenig, & Kelly, 2016) can tilt plant–scatterhoarder interactions towards mutualism. We briefly discuss this possibility in Bogdziewicz, Crone, et al. (2020), giving pros and cons for the occurrence of such shifts in our study system. Furthermore, we agree with the pilferage-based mechanism

for changes in interaction outcomes that was outlined by Moore and Dittel (2020). In fact, this was the subject of an earlier paper by our group (Zwolak, Bogdziewicz, Wróbel, & Crone, 2016). For at least one species pair, European beech *Fagus sylvatica* and yellow-necked mice *Apodemus flavicollis*, the interaction seems to change from antagonistic in non-mast years to mutualistic in mast years, with the outcome driven by fluctuations in the probability of cache pilferage (from high in non-mast years to low in mast years: Zwolak et al., 2016).

Trees can live for hundreds of years and the temporal scale of most research studies is one or even two orders of magnitude less than plant life spans. Thus, understanding the net effect of the interaction over a tree's lifetime would require understanding the frequency of mast- and non-mast years, as well as how the consumer populations change through time (cf. Moore & Dittel, 2020; Zwolak et al., 2016). It would also be useful to know how different life stages are affected by dispersal, competition and seed burial, and to integrate these effects throughout a plant's life span using life cycle models (e.g. Elwood, Lichti, Fitzsimmons, & Dalglish, 2018). The effects of variation in seed production on lifetime plant fitness and forest population dynamics would be a particularly fruitful area for more empirically based modelling studies. We hope that these would identify key hypotheses that could be tested in experiments over feasible research time-scales.

#### 5 | CONCLUSIONS

Ecological research has a long history of isolating one process at a time while leaving others constant, regardless of whether researchers use experimental or modelling approaches. In experiments, it is common to look at one factor at a time. In the models we use to interpret the net effects of synzoochory for plants, we have so far isolated the net effect of synzoochory for seedling establishment. In the oak–mouse systems that inspired these comments (Bogdziewicz, Crone, et al., 2020), we believe that quantitative evaluation of the factors that contribute to this life stage (seed burial, seed dispersal distance and seed consumption rates) provides a more comprehensive picture of the interaction than less-quantitative approaches (e.g. counting the number of positive and negative effects, Gómez et al., 2019). We applaud the notion of further research about the costs and benefits of synzoochory for other plant populations. Even for the same species, we might see different responses in different ecological contexts. We look forward to the possibility of more systematically comparing the net outcome of this interaction across a broader array of ecological systems.

#### ACKNOWLEDGEMENTS

R.Z. was supported by Polish National Science Centre Grant 'Harmonia' No. 2018/30/M/NZ8/00052. M.B. was supported by Polish National Science Centre grant 'Preludium' No. 2015/17/N/NZ8/01565.

## AUTHORS' CONTRIBUTIONS

R.Z., M.B. & E.E.C. conceived and wrote the paper.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13463>.

## DATA AVAILABILITY STATEMENT

This article does not contain data.

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**How to cite this article:** Zwolak R, Bogdziewicz M, Crone EE.

On the need to evaluate costs and benefits of synzoochory for plant populations. *J Ecol.* 2020;00:1–5. <https://doi.org/10.1111/1365-2745.13463>