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TECHNICAL NOTE

Seed predator effects on plants: Moving beyond time-corrected proxies

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Abstract

We previously demonstrated that small mammals impact plant recruitment globally via size-dependent seed predation, generating a unimodal pattern across ecosystems. Chen et al. (2021) critiqued our seed removal analysis, advocating corrections for exposure time. We show such manipulations are unwarranted and argue for increased emphasis on plant recruitment metrics.

KEYWORDS
coexistence, consumer effects, granivory, plant recruitment, seed predation, seed size

INTRODUCTION

In our recent global analysis, we demonstrated that size-dependent, post-dispersal seed predation by small mammals significantly impacts plant recruitment around the world (Dylewski et al., 2020). Moreover, we found differential effects of small mammal seed predation across ecosystems such that seed predator impacts were greatest for larger-seeded species in small-seeded systems (e.g., grasslands) and for smaller-seeded species in large-seeded systems (e.g., tropical forests), generating a unimodal global pattern. Our analyses emphasised seed sowing experiments that directly measure effects of seed predation on plant recruitment, but we also evaluated seed removal studies as proxies for seed predator effects on plants, as such studies represent the bulk of the research available to date. Chen et al., (2021) challenged our seed removal results on several technical points. However, their critique is misguided, as our meta-analysis of seed sowing experiments yielded similar results while directly measuring seed predator effects on plant recruitment. Moreover, as we show, the data manipulation they propose to "correct for bias" does not change our results. Herein, we (1) establish the importance of seed sowing experiments over seed removal studies for evaluating seed predator effects on plants and (2) address the flaws in Chen et al.'s critique of our seed removal results.

Although far too rare, *in situ* experiments that manipulate seed predator access to sown or naturally dispersed seeds clearly demonstrate (individually and via meta-analyses in Dylewski et al., 2020) that small mammal seed predators can have strong effects on plant recruitment, populations and community structure via size-dependent seed predation (e.g., Brown & Heske, 1990; Chen & Valone, 2017; Howe & Brown, 2001; Maron et al., 2012; Reader, 1993). Importantly, these seed-sowing experiments overcome problems with seed removal studies raised by Chen et al., 2021 like effects of exposure time because seeds are generally sown during dispersal and left until germination, thereby representing

natural exposure windows, environmental context, etc. Moreover, seed sowing experiments provide a more direct metric for establishing whether seed predation actually matters for plant recruitment and for which species. This is essential because many factors can undermine the effects of seed predation on plant recruitment including lack of seed limitation and post-emergence seedling mortality due to density dependent biotic factors or density independent abiotic stressors (Crawley, 2000). As discussed in Dylewski et al., (2020), seed sowing experiments are generating profound revelations about how size-dependent seed predation can influence coexistence between large- and small-seeded plant species and how these processes can differ by ecological context.

Seed offering trials, which measure relative seed removal rates, provide a valuable tool for assessing short-term seed predator preferences. However, their usefulness for indexing seed predator effects on plant recruitment has long been questioned (Edwards & Crawley, 1999). The eight known studies pairing seed offerings with seed sowing experiments find that seed removal rates sometimes crudely predict seed predator effects on plant recruitment, but not consistently (e.g., Edwards & Crawley, 1999; Dirzo et al., 2007; Zwolak et al., 2010, see Dylewski et al., 2020). Hence, Chen et al.'s focus on seed removal over seed sowing experiments is misplaced. Moreover, their advocated approach is unwarranted and misleading as presented. In applying their "correction" for exposure time to our seed removal data using reference points of 1, 3, and 12 days (the average exposure time across studies), it can be seen that (1) the unimodal seed-size relationship is always present and (2) the height of the curve increases with exposure time (Figure 1). Chen et al. chose the 1-day mark and then concluded that the relationship was "likely of limited biological significance" because the curve was diminished. Given that seed predation is a cumulative process and the average exposure time across studies was 12 days, their interpretation is misleading at best. Notably, applying their correction at the 12-day mark generates a higher peak than our "uncorrected" data. As we show here, manipulating the data as proposed by Chen et al. is unwarranted. In our original approach, we took more efficient and objective steps to control for study-level variation in background factors like exposure time (see Appendix S1 and Dylewski et al., 2020). Overall, critiques by Chen et al. were largely without merit, but for transparency we address each in Appendix S1.

In sum, Chen et al.'s criticism is misguided. Understandings of seed predator effects on plants will not be advanced by developing unwarranted corrections

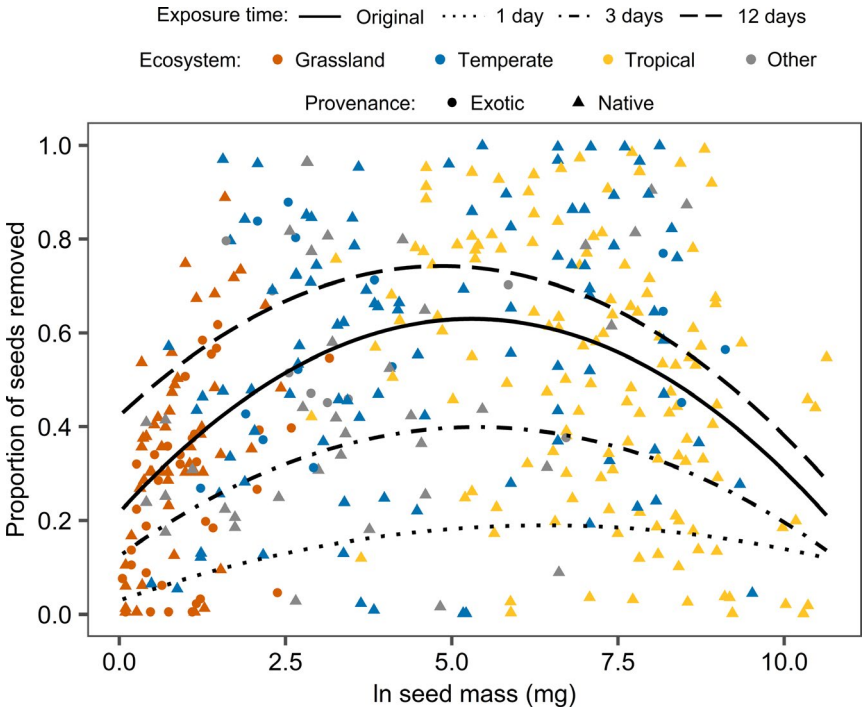

FIGURE 1 Predicted relationships between small mammal seed removal rates and seed mass (ln [mg +1]), as assessed using the data from our global literature review (Dylewki et al. 2020) in their original form (solid dark line) or after "correcting" for exposure time (dashed lines) following Chen et al.,'s (2021) method, which assumes an exponential decline in seed survival over time. We applied their correction at different seed exposure times: 1 day (as used in their critique), 3 days and 12 days (the average exposure time across studies). In all cases, the unimodal relationship remained significant (seed mass: $p < 0.0005$, seed mass^2: $p < 0.005$; see Table S1). While Chen et al. present the 1-day depiction to argue that the pattern had been greatly weakened after applying their correction, it can be seen that the height of the resultant curve is simply a function of the chosen exposure time. Following the style of Dylewki et al.'s (2020) Figure 2, data points represent residual variance in seed removal values after accounting for the random effect of study predicted from the original model

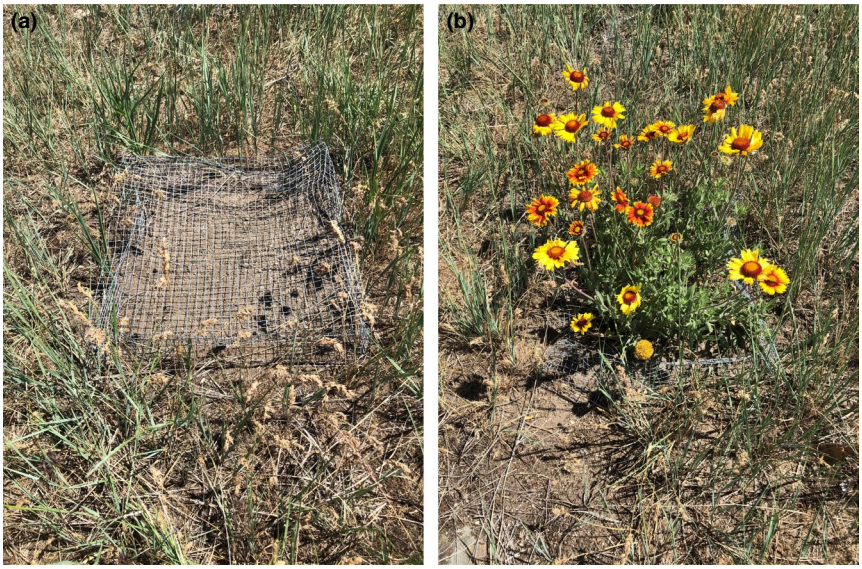

FIGURE 2 An example of one type of seed sowing experiment showing paired seed cages (40 × 40 cm spaced 40 cm apart) allowing (left: note "doors" cut into cage sides) or excluding (right: no doors) rodent access to equal numbers of seeds sown in each cage (this method dates back to Hulme, 1994 if not earlier). Results demonstrate rodent effects on recruitment of the large-seeded native blanket flower (*Gaillardia aristata*) in Intermountain grasslands of the western U.S. This experiment was repeated the following year, and, while rodent seed predation effects were still strong and significant, far fewer plants established due to dry spring weather overriding survival of many seedlings that escaped seed predation, i.e. density-independent abiotic mortality dampened rodent effects on plant recruitment (Pearson et al. in review). Interestingly, Edwards and Crawley (1999) similarly found that seed predators strongly affected plant recruitment when conditions were good, but that other processes linked to microsite availability and density dependent seedling survival could usurp these effects. Such effects cannot be assessed using seed offerings. (Note, cage tops are removed after emergence, but the open cage top was retained as there were no seedlings)

to apply to uncertain proxies. Improving knowledge of seed predator effects on plant recruitment, populations, and community structure will require more studies that experimentally manipulate consumer access to seeds sown under realistic conditions (Dylewski et al., 2020; Larios et al., 2017; Figure 2). Refining such approaches to better differentiate seed predator identity and manipulate seed traits, seed density and other relevant factors will greatly advance understandings of these important consumer effects on plants.

AUTHORSHIP

DEP drafted the main text. YKO drafted the Appendix and lead on analyses with inputs from all. All authors contributed to writing and refining the final document.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data reposited in the Dryad archive: https://doi.org/10.5061/dryad.hqbzkh1fp.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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