A model for seed mass variation

A resource competition model for seed mass variation in grasslands

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Running title: a model for seed mass variation
SUMMARY

1. The large variation in seed mass among species inspired a vast array of theoretical and empirical research that attempt to explain this variation. So far, seed mass variation was explained by two classes of models, the first focused on coexistence of species varying in seed mass within communities, while the second focused on variation in seed mass between communities along environmental gradients.

2. Here, we develop a mechanistic resource competition model capable of simultaneously explaining variation in seed mass within and between communities. The model is based on two basic processes, biomass growth and biomass removal, and incorporates two fundamental aspects that have been overlooked by most previous models: light asymmetry (higher light acquisition per unit biomass for larger individuals) and growth allometry (negative dependency of relative growth rate on plant biomass).

3. We use the model to investigate how differences in seed mass among species interact with light asymmetry and growth allometry to determine the relative fitness (relative reproductive success) of large- vs. small-seeded species within communities, and how such interactions are translated into patterns of seed mass variation along gradients of resource availability and disturbance.

4. Under the framework of the model, growth allometry increases the relative fitness of small seeded species while light asymmetry increases the relative fitness of large seeded species. Increasing resource availability increases the fitness of large-seeded species by increasing the relative importance of light competition. In contrast, disturbance increases the fitness of small seeded species due to a combination of different mechanisms operating simultaneously.

5. Resource availability and disturbance also influence the magnitude of within-community differences in fitness (and therefore, the potential for species coexistence). The observed patterns are consistent with empirically observed
A model for seed mass variation

responses of species diversity to resource availability, disturbance and their interaction (e.g. the unimodal diversity response to resource availability and the 'grazing reversal hypothesis').

6. The ability of this simple model to explain a wide range of patterns that were previously explained by different classes of models suggests that the mechanisms captured by the model are important in determining patterns of grassland diversity.

Key words: allometric growth, size-asymmetric competition, competition-colonization trade-off, disturbance, functional traits, productivity, relative growth rate, species diversity, seed size-number trade-off
INTRODUCTION

The large variation in seed mass within and between plant communities has fascinated ecologists for decades (Salisbury 1942; Harper, Lovell & Moore 1970; Baker 1972; Moles et al. 2007). Explaining this variation is crucial for understanding the structure and diversity of plant communities because seed mass is an essential component of plant fitness, affecting competitive ability (Turnbull, Rees & Crawley 1999; Leishman 2001; Turnbull et al. 2004), tolerance to environmental stressors (Baker 1972; Leishman & Westoby 1994; Osunkoya et al. 1994; Saverimuttu & Westoby 1996), seed predation (Thompson 1987), as well as dispersal (Greene & Johnson 1993) and dormancy (Harel, Holzapfel & Sternberg 2011). Moreover, since the amount of resources available for reproduction is never unlimited, there is an inherent trade-off between seed mass and seed number, and any investment in seed mass must come at the expense of offspring number (Smith & Fretwell 1974). This inherent trade-off has important evolutionary and ecological implications (e.g. Rees & Westoby 1997; Eriksson & Eriksson 1998; Coomes et al. 2002; Falster, Moles & Westoby 2008; Ben-Hur et al. 2012).

Previous attempts to explain variation in seed mass have focused on two distinct questions: (1) what mechanisms are capable of maintaining coexistence of species with different seed mass within a community (e.g. Rees & Westoby 1997; Eriksson & Eriksson 1998; Leishman & Murray 2001; Coomes et al. 2002; Franzen 2004; Turnbull, Rees & Purves 2008; Cornwell & Ackerly 2009; Muller-Landau 2010; Ben-Hur et al. 2012; Lonnberg & Eriksson 2012; D’Andrea, Barabas & Ostling 2013) and (2) what mechanisms generate variation in seed mass between communities (e.g. Fernandez Ales, Laffarga & Ortega 1993; Pakeman et al. 2008; Schamp, Chau & Aarssen 2008; Metz et al. 2010; Viard-Cretat et al. 2011; Bernard-Verdier et al. 2012;
A model for seed mass variation

Carmona et al. 2015; Lhotsky et al. 2016). Although these components of seed mass variation are strongly interconnected, mechanisms maintaining variation within communities have usually been studied independently of mechanisms accounting for between-community variation, and no attempt has been made to develop a theoretical framework capable of simultaneously explaining both aspects of variation.

Here we present for the first time a theoretical framework that attempts to simultaneously explain both phenomena. While the basic mechanisms and processes incorporated in the proposed framework are general, the manner by which we model plant growth and disturbance was fitted to herbaceous plants since much of the previous theoretical (Rees & Westoby 1997; Levine & Rees 2002; Turnbull, Rees & Purves 2008; Venable & Rees 2009) and empirical (Maranon & Grubb 1993; Eriksson 2005; Metz et al. 2010; Viard-Cretat et al. 2011; Bernard-Verdier et al. 2012; Ben-Hur & Kadmon 2015; Carmona et al. 2015) studies of seed mass variation have focused on grassland communities.

Our paper is organized in four parts. In the first part, we outline some limitations of current models of seed mass variation. In the second part, we develop our theoretical model. In the third part, we use the model as a framework for analyzing the mechanisms underlying variation in seed mass within and between communities. In particular, we focus on the role of resource availability and disturbance because empirical studies indicate that these two factors are major determinants of seed mass variation in grassland communities (e.g. Fernandez Ales, Laffarga & Ortega 1993; Metz et al. 2010; Pakeman 2011; Bernard-Verdier et al. 2012; Carmona et al. 2015; Lhotsky et al. 2016). Finally, we discuss our theoretical results with respect to previous theoretical and empirical studies of seed mass variation.
A model for seed mass variation

Limitations of existing models

The enormous variation of seed mass in plant communities has attracted much theoretical interest because it contrasts the intuition that seed mass of species inhabiting the same habitat should converge into some 'optimal' value (Smith & Fretwell 1974). Most models attempting to explain this variation assume a trade-off between seed mass and seed number, where large seeds have some advantage which compensates for their lower number. Depending on the model, this advantage might be a higher competitive ability (the 'competition-colonization trade-off hypothesis', Rees & Westoby 1997; Geritz, van der Meijden & Metz 1999; Turnbull, Rees & Crawley 1999; Turnbull et al. 2004), or higher tolerance to environmental stress (the 'tolerance-fecundity trade-off hypothesis', Muller-Landau 2010; Adler et al. 2013; D'Andrea, Barabas & Ostling 2013; Haegeman, Sari & Etienne 2014). In both cases, different combinations of seed mass and seed number may lead to stable coexistence.

A fundamental assumption in most of these models is that the total amount of resources available for reproduction is constant among species, creating a trade-off between seed size and seed number (Smith & Fretwell 1974; Rees & Westoby 1997; Coomes & Grubb 2003; Muller-Landau 2010). While this assumption is a reasonable approximation in some communities, coexisting species often show considerable differences in both their adult size and reproductive biomass (Falster, Moles & Westoby 2008). Nevertheless, little attention has been paid to the manner by which such differences affect the expected patterns of seed mass variation (though see Falster, Moles & Westoby 2008; Venable & Rees 2009).
A model for seed mass variation

More importantly, most of these models assume, rather than show, that large seeds provide a certain kind of advantage. A more mechanistic approach should elucidate the mechanisms and interactions that generate this variation (Adler et al. 2013). In other words, the advantage of large seeds in acquiring resources, suppressing competitors, or tolerating low resource levels, should be established rather than assumed by the model. So far, very few models have incorporated such a mechanistic approach (but see Tilman 1988).

Two factors that might be particularly important in determining patterns of seed mass variation in plant communities are the size-asymmetry of light competition (the fact that tall individuals receive more light per unit biomass than short individuals), and the allometry of plant growth (the fact that small-seeded species have higher relative growth rate (RGR) than large-seeded species). The size-asymmetry of light competition (hereafter ‘light asymmetry’) has long been recognized as a crucial determinant of the fate of small-seeded vs. large-seeded species (Tilman 1988; Schwinning & Fox 1995) but has rarely been taken into account in models of seed size variation. Moreover, most empirical studies of between-community variation in seed mass have focused on gradients of soil resource availability (hereafter, ‘resource availability’) and disturbance, assuming that these factors affect the relative importance of above- vs. belowground competition and therefore the relative fitness of large-seeded vs. small-seeded species (e.g. Fernandez Ales, Laffarga & Ortega 1993; Metz et al. 2010; Pakeman, Lennon & Brooker 2011; Bernard-Verdier et al. 2012; Carmona et al. 2015; Lhotsky et al. 2016). Still, this chain of causal relationships has never been tested within the framework of an explicit model.
A model for seed mass variation

Growth allometry is another universal phenomenon (Turnbull et al. 2012) expected to influence the relative success of small-seeded vs. large-seeded species within the same community, as well as the patterns and magnitude of variation in seed mass along gradients of resource availability and disturbance (Maranon & Grubb 1993). Nevertheless, models of seed mass variation have rarely considered whether and how growth allometry affects variation in seed mass (but see evolutionary model by Falster, Moles & Westoby 2008).

In this study we develop a resource competition model that explicitly incorporates differences among species in seed mass, growth allometry and light asymmetry. We then use our model to investigate the manner by which light asymmetry, growth allometry, resource availability, and disturbance, affect the relative fitness of species with varying seed mass, and how such differences are ‘translated’ into patterns of seed mass variation within and between communities.

**THE MODEL**

The model is an extension of a general resource competition model that simulates the growth of \( n \) individual plants that compete for \( m \) shared resources (DeMalach et al. 2016). In contrast to most previous models of seed mass variation that focused on evolutionary processes, we focus on ecological timescales, and investigate the mechanisms by which existing differences in seed mass among species interact with environmental factors in determining the relative fitness of species with different seed sizes within communities, and the consequences of such interactions for patterns of seed mass variation along environmental gradients. Importantly, our model does not assume that all species in the community have the same reproductive mass (the assumption behind the seed size – number trade-off).
A model for seed mass variation

According to the model, the biomass ($S$) of individual $i$ in time step $(t+1)$ is determined by its biomass in time $(t)$, its maximal relative growth rate ($\mu$, the growth rate per unit biomass [RGR] in the absence of any resource limitation), and a parameter $p$ indicating the degree to which growth rate is reduced by resource limitation:

(1) \[ S_{i(t+1)} = S_{i(t)} + S_{i(t)} \cdot \mu_i \cdot p_{i(t)}. \]

We assumed that a single resource $j$ limits the growth of each plant at each time step, that the identity of the limiting resource may change over time depending on the availability of all various resources, and that the limiting resource at time $(t)$ is determined by Liebig’s law of the minimum:

(2) \[ p_{i(t)} = \min\left(\frac{r_{i(t)}}{k + r_{i(t)}}, \frac{r_{ji(t)}}{k + r_{ji(t)}}, \ldots, \frac{r_{mi(t)}}{k + r_{mi(t)}}\right). \]

This expression is based on a Michaelis-Menten (Monod) growth equation, where the value of $p$ ranges from zero (no growth) to one (maximal growth), $k$ is the half saturation constant, and $r_{ji(t)}$ is the net amount of resource $j$ available per unit biomass of individual $i$ at time $(t)$, after taking into account a resource-specific maintenance cost:

(3) \[ r_{ji(t)} = \frac{R_{ji(t)}}{S_{i(t)}} - M_{ji}. \]

$R_{ji(t)}$ is the amount of resource $j$ available for the whole plant at time $(t)$, $M_{ji}$ is a parameter indicating the maintenance cost of resource $j$ for individual $i$, and $r_{ji(t)}$ is the net amount of resource $j$ available per unit biomass after taking into account the
A model for seed mass variation

maintenance cost. If maintenance cost \((M)\) exceeds the amount of resource available per unit biomass \((R/S)\), growth rate is set to zero (i.e. no negative growth).

It is further assumed that each resource is supplied at some constant rate and that the amount of resource \(j\) available for plant \(i\) at a given time step \(R_{ji(t)}\) is determined by the size-asymmetry of resource exploitation (Schwinning & Weiner 1998):

\[
(4) \quad R_{ji(t)} = \bar{R}_j \cdot \frac{S_{i(t)}^\theta}{\sum_{i=1}^{n} S_{i(t)}}
\]

where \(\bar{R}_j\) is the supply rate (total amount of resource \(j\) supplied to the system at each time step), and \(\theta\) indicates the level of size asymmetry in resource exploitation. When \(\theta = 1\), resource exploitation is completely size symmetric (each plant gets the same amount of resource per unit biomass), whereas as \(\theta\) increases, resource exploitation becomes more asymmetric and larger plants get larger amounts of resource per unit biomass than smaller plants. Previous analyses of this resource competition model have shown that it is highly robust to a wide range of simplifying assumptions (DeMalach et al. 2016).

Here we extend this model by incorporating three additional elements to the basic model: growth allometry, disturbance, and seed production. Growth allometry is introduced by adding a coefficient of allometry \((a)\) to the growth rate ranging from zero to one, where one leads to size independent RGR and values smaller than one lead to allometric growth (i.e. a reduction in RGR with increasing size). Note that absolute growth rate increases with size also under allometric growth.

Disturbance is introduced by adding a component of biomass removal to the growth model. This procedure adopts Grime's (1979) definition of disturbance as "a
A model for seed mass variation

mechanism which limits plant biomass by causing its partial or total destruction”.

The portion of biomass removed by disturbance is a function of two elements: the intensity of disturbance \((D, \text{ where } D = 0 \text{ implies no disturbance})\); and the degree of size-dependency of the disturbance \((b, \text{ where } b = 0 \text{ implies that disturbance is size-independent and increasing } b \text{ implies that large individuals loose higher proportions of their biomass than smaller ones (e.g. as in mowing or grazing by large herbivores)})\).

These two extensions lead to the following model:

\[
S_{i(t+1)} = S_{i(t)} + a \cdot \mu_i \cdot \min \left( \frac{r_{i1(t)}}{k+r_{i1(t)}}, \ldots, \frac{r_{im(t)}}{k+r_{im(t)}} \right) - D \cdot S_{i(t)}^b
\]

where \(a\) is the allometry parameter, \(D\) indicates the intensity of disturbance and \(b\) indicates its size-dependency.

Finally, we assumed that at the end of the growing season, each individual produces \(O\) seeds by allocating some proportion \((\alpha)\) of its biomass to reproduction. Thus, the reproductive success of individual \(i\) equals:

\[
O_i = \alpha \cdot \frac{S_{i(\text{end})}}{S_{i(0)}}
\]

where \(O_i\) is the number of seeds produced per plant, \(S_{i(\text{end})}\) is the final biomass, \(S_{i(0)}\) is the initial (seed) biomass, and \(\alpha\) is the proportion of biomass allocated to reproduction.

**METHODS**

We used our model to investigate the role of growth allometry \((a)\), light asymmetry \((\theta_{\text{light}})\), resource availability \((\bar{R}_{\text{soil}})\), disturbance intensity \((D)\) and disturbance size-dependency \((b)\) on the reproductive success of species competing for both light and
A model for seed mass variation

soil resources. Soil resources were exploited symmetrically (i.e. $\theta_{\text{soil}} = 1$) in all simulations. To simplify interpretation, each individual had a different seed mass that was drawn from a lognormal distribution ($\text{mean} = -1$ and $\text{SD} = 1.5$). Thus, each individual was interpreted as a different 'species' (or 'functional type') and all species were identical in all traits except for their seed mass (see table 1 for all other parameters). A measure of relative fitness ($F$) was determined for each 'species' by dividing its reproductive success by the total seed production of all species in the community:

\[
F_i = \frac{O_i}{\sum_{k=1}^{n} O_k}.
\]

This definition of fitness differs from some definitions used in evolutionary biology (Adler et al. 2013; Kraft, Godoy & Levine 2015) but is almost equivalent to the definition of Smith & Fertwell (1974) in their classical paper on seed mass evolution (Appendix S1).

Based on the calculations of relative fitness we also determined for each community the community weighted mean (CWM) seed mass (Bernard-Verdier et al. 2012):

\[
\text{CWM} = \sum_{i}^{n} F_i S_{i(0)}.
\]

**Effects of growth allometry and light-asymmetry**

In all analyses we simulated the growth of 100 species under competition for both light and soil resources. The first analysis focused on within-community variation and was designed to test whether and how growth allometry ($a = 0.5, 0.75, 1$) and light asymmetry ($\theta_{\text{light}} = 1, 1.15, 1.3$) affect the relative fitness of species varying in their seed mass. We hypothesized that both factors are important in determining the
A model for seed mass variation

relative fitness of species in the community but work in opposite directions, with growth allometry increasing the relative fitness of small-seeded species and light asymmetry increasing the relative fitness of large-seeded species. These simulations were performed under constant environmental conditions \( \bar{R}_{\text{soil}} = 100, D = 0 \), thereby, focusing on seed mass variation \textit{within} communities. In further simulations we mostly focused on seed mass variation \textit{between} communities and the manner by which it is influenced by resource availability and disturbance.

**Effects of resource availability**

A second set of analyses focused on the effects of resource availability \( \bar{R}_{\text{soil}} = 50, 100, 150, 250 \) on relative fitness of species varying in their seed mass. Following results from the first set of analyses indicating that both growth allometry and light asymmetry affect relative fitness, these simulations were performed under a ‘factorial design’ of growth allometry \((a = 1 \text{ and } 0.75)\) and light asymmetry \((\theta_{\text{light}} = 1 \text{ and } 1.15)\).

We expected that increasing resource availability would increase the fitness of large-seeded species and decrease the fitness of small-seeded species. However, assuming that the competitive advantage of large-seeded species increases with increasing light asymmetry and decreases with increasing growth allometry, we expected that the degree to which increasing resource availability facilitates the fitness of large-seeded species would increase with increasing light asymmetry and decrease with increasing growth allometry.

**Effects of disturbance**

A third set of simulations was performed to investigate the effects of disturbance on the relative fitness of species varying in seed mass. Two aspects of the disturbance regime were tested for their effects: the intensity of disturbance \((D = 0, 0.05, 0.01, \text{ etc.})\).
A model for seed mass variation

0.02) and its size dependency \( (b = 1, 1.05, 1.1) \). Resource availability was kept constant at an intermediate level \( (\bar{R}_{soil} = 100) \) in these simulations. We expected that increasing disturbance would increase the relative fitness of small-seeded species and that the magnitude of this effect would be higher under size-dependent disturbance (i.e. when disturbance has a stronger negative effect on the biomass of large plants).

**Interaction between the effects of resource availability and disturbance**

A fourth set of analyses was performed to test the hypothesis that disturbance interacts with resource level in determining the performance of large- vs. small-seeded species. In this analysis we tested the combined effects of disturbance intensity \( (D = 0, 0.01, 0.02) \) and resource availability \( (\bar{R}_{soil} = 50, 100, 150, 250) \) on relative fitness of species with varying seed mass while holding the size-dependency of disturbance constant \( (b = 1.1) \).

A final set of analyses was performed to explore the effects of disturbance and resource availability on community weighted mean (CWM) seed mass. In these analyses we evaluated the response of CWM seed mass to a gradient of resource availability \( (\bar{R}_{soil} = 30 - 250) \) under different levels of disturbance intensity \( (D = 0, 0.01, 0.02) \). These analyses were performed under fixed levels of light asymmetry \( (\theta_{light} = 1.3) \), growth allometry \( (a = 0.75) \), and size dependency of disturbance \( (b = 1.05) \).

**RESULTS**

The model results are presented as the relationship between seed mass and relative fitness of all species in the community with species ranked according to their seed mass (hereafter, ‘fitness-seed mass relationship’, Fig. 1). Each simulation generates a
A model for seed mass variation

unique fitness-seed mass relationship that represents a particular parameter regime. This visualization has three advantages. First, the value of seed mass that maximizes relative fitness indicates the optimal seed mass 'strategy' under the relevant conditions (Fig. 1). A shift in this value in response to a particular parameter (e.g. disturbance intensity) indicates a shift in the optimal seed-mass strategy. Second, since relative fitness of all species sums to one, this visualization facilitates comparison of fitness-seed mass relationships obtained for different combinations of ecological conditions. Third, the maximum height of the fitness-seed mass relationship is equivalent to the Berger-Parker index (BPI) of dominance (Berger & Parker 1970) and can be interpreted as a measure of fitness differences among species in the community. Everything else being equal, increasing BPI values implies a lower potential for coexistence of large-seeded and small-seeded species (Adler et al. 2013; Kraft, Godoy & Levine 2015).

Effects of light-asymmetry and growth allometry

Both light asymmetry and growth allometry affect the fitness-seed mass relationship (Fig. 2). If competition is size-symmetric ($\theta_{\text{light}} = 1$) and relative growth rate is isometric ($a = 1$), seed mass does not affect fitness and all species have the same fitness regardless of their seed mass (i.e. a fully neutral community, Fig. 2a). Increasing light asymmetry under isometric growth ($a = 1$) provides a competitive advantage for large-seeded species and increases their fitness relative to small-seeded species resulting in a monotonic increase of relative fitness with increasing seed mass (Fig. 2a-c). Increasing allometry (i.e. decreasing $a$) under size-symmetric light competition ($\theta_{\text{light}} = 1$) has an opposite effect and increases the fitness of small-seeded species, resulting in a monotonic decline of relative fitness with increasing seed mass (Fig. 2a, d, g). Under the more realistic scenario of asymmetric light competition
A model for seed mass variation

\((\theta_{\text{light}} > 1)\) and allometric growth \((a < 1)\), neither force dominates the pattern of variation and relative fitness may show a unimodal response to variation in seed mass with maximum fitness for intermediate seed mass. In such cases, the optimal strategy (i.e. the level of seed mass that maximizes fitness) increases with increasing light asymmetry (compare Fig. 2e, f) and decreases with increasing allometry (compare Fig. 2e, i).

**Effects of resource availability**

The effect of resource availability on the fitness-seed mass relationship depends on the competitive regime and the allometry of growth. If competition is size-symmetric and relative growth rate is isometric (Fig. 3a), the fitness-seed mass relationship remains flat (neutral) and is unaffected by resource availability. If competition is size-asymmetric and relative growth rate is isometric (Fig. 3b), increasing resource availability increases the relative fitness of large-seeded species. If competition is size-symmetric and relative growth rate is isometric (Fig. 3c), the fitness-seed mass relationship decreases monotonically and increasing resource availability increases the relative fitness of small-seeded species. If competition is size-asymmetric and relative growth rate is allometric (Fig. 3d), relative fitness shows a unimodal response to variation in seed mass and the seed mass that maximizes fitness increases with increasing resource level.

**Effects of disturbance**

Both characteristics of the disturbance regime (intensity and size dependency) have a strong effect on the fitness-seed mass relationship (Fig. 4). Increasing disturbance intensity \((D)\) shifts the level of seed mass that maximizes fitness to lower levels, thereby facilitating the relative fitness of small-seeded species (Fig. 4). This result is
A model for seed mass variation

obtained even if disturbance is size-independent \((b = 1, \text{Fig. 4a})\). Increasing the size-dependency of disturbance \((b)\) while keeping disturbance intensity constant has a similar effect (Fig. 4b).

**Interactions between the effects of resource availability and disturbance**

There is a strong interaction between the effects of disturbance and resource availability on the fitness-seed mass relationship (Fig. 5). In general, increasing disturbance reduces the degree to which increasing resource availability facilitates the relative fitness of large-seeded species (Fig. 5). This interaction is translated to corresponding effects on community weighted mean (CWM) seed mass (Fig. 6a). In general, CWM seed mass increases with increasing resource availability and decreases with increasing disturbance intensity (Fig. 6a). However, the two factors interact, with the strongest effect of resource availability on CWM seed mass occurring at intermediate levels of disturbance. Weakening disturbance intensity reduces the magnitude of this effect by increasing the CWM seed mass of communities under low resource levels, while strengthening disturbance intensity reduces this effect by lowering the CWM seed mass of communities under high resource levels (Fig. 6a).

Resource availability and disturbance also interact in their effects on the magnitude of fitness differences among species (as expressed by the Berger-Parker index, Fig. 6b). Under low resource levels, the effect of disturbance is positive, while under high resource levels it has a U-shaped effect (i.e. lowest value under intermediate disturbance). Increasing resource availability has a U-shaped effect on the magnitude of fitness differences at the absence of disturbance, but a negative effect under moderate and intense disturbances (Fig. 6b).
DISCUSSION

We investigated mechanisms and consequences of seed mass variation within and between communities using a simple model of multiple species competing for both soil and light resources. A novel feature of our model is an explicit incorporation of growth allometry and size-asymmetric light competition, two fundamental characteristics of plant growth that have been ignored in most previous models of seed mass variation. Our most novel result is that small-seeded species may attain a similar and even higher fitness than larger-seeded species under both symmetric and asymmetric competition without having any intrinsic advantage (such as higher fecundity [Muller-Landau 2010], higher colonization ability [Rees & Westoby 1997], or higher tolerance to seed predation [Tilman 1988]). This result is derived from growth allometry, a universal and strongly documented phenomenon (Paine et al. 2012; Turnbull et al. 2012), while the mechanisms incorporated in previous models are more contingent and are less supported by empirical studies.

Despite its simplicity, our model is capable of explaining a variety of empirically observed patterns of seed mass variation that have previously been explained by different models or different hypotheses. Our overall results point to the following generalizations:

1. Growth allometry increases the fitness of small-seeded species, while light asymmetry increases the fitness of large-seeded species.

2. Increasing resource availability increases the relative fitness of large-seeded species thereby increasing CWM seed mass. In contrast, disturbance increases the relative fitness of small-seeded species thereby decreasing CWM seed mass.
A model for seed mass variation

3. The effect of resource availability on fitness differences is U-shaped at the absence of disturbance and negative under disturbance. The effect of disturbance is positive under low resource levels, but U-shaped under high resource levels.

Below we discuss the main results of the model in comparison with previous theoretical and empirical studies of seed mass variation. We conclude by suggesting that our modelling approach may provide a promising route for improving the theoretical basis of 'trait based ecology' (McGill et al. 2006; Shipley et al. 2016).

**Within-community variation**

Early models attempting to explain the enormous variation in seed mass within plant communities assumed a competitive advantage of large-seeded species and demonstrated that such advantage could explain coexistence of large-seeded and small-seeded species through a competition-colonization trade-off (e.g. Rees & Westoby 1997; Geritz, van der Meijden & Metz 1999). In contrast to this approach, our model starts from a mechanistic description of plant growth and resource acquisition, and the competitive advantage of large- vs. small-seeded species arises from the fundamental characteristics of plant growth, rather than assumed. The model confirms the assumption that a large seed mass may lead to competitive advantage, but demonstrates that this advantage is far from being universal, and depends on the degree of growth allometry and size-asymmetry of light competition (Fig. 2). This result is important, because growth allometry is a fundamental element of plant growth (Turnbull et al. 2012), size asymmetry is a fundamental property of light competition (Schwinning & Weiner 1998; DeMalach, Zaady & Kadmon 2017), and the two factors operate in opposite directions in determining the fitness of large- vs. small-seeded species (Fig. 2).
A model for seed mass variation

Moreover, our results indicate that the balance between the contrasting effects of growth allometry and size asymmetry depends on resource availability (Fig. 3). Increasing resource availability increases the relative importance of light competition (which is size-asymmetric), and therefore increases the relative fitness of large-seeded species. Thus, in contrast to previous models assuming that large-seeded species had a universal competitive advantage over small-seeded species, our model predicts that such competitive advantage is limited to situations of high resource availability where light is the dominant limiting factor.

The most fundamental difference between our model and previous competition-colonization models is that the advantage of small-seeded species is related to growth allometry rather than higher colonization rates. Such advantage has a much stronger empirical support (Paine et al. 2012; Turnbull et al. 2012) and does not require strict competitive hierarchy as assumed by models of competition-colonization trade-off (Coomes & Grubb 2003).

An alternative class of trade-off models attributes the advantage of large-seeded species to higher fitness under environmentally stressful conditions (Muller-Landau 2010; D'Andrea, Barabs & Ostling 2013; Haegeman, Sari & Etienne 2014). Like most competition-colonization models, these models lack an explicit consideration of individual growth and competition, thereby ignoring the potential consequences of growth allometry and light-asymmetry. It should also be noted that in contrast to competition-colonization models (and our model), a key element of these models is spatial heterogeneity in ecological conditions. Analysing the consequences of such heterogeneity is beyond the scope of our work, but in the appendix we show that our theoretical framework can easily accommodate a size-dependent modifier of survival
A model for seed mass variation that increases the ability of large-seeded species to tolerate low resource levels, as assumed by this class of models (Appendix S2).

Finally, it should be noted that both classes of trade-off models assume that reproductive biomass is fixed and equal for all species in the community (e.g. Smith & Fretwell 1974; Rees & Westoby 1997; Coomes & Grubb 2003; Muller-Landau 2010). Thus, these models apply to communities where species differ in their seed mass, but have a similar adult biomass. In contrast, in our model, adult mass is determined by seed mass and the rate of plant growth as determined by resource availability, competition, and disturbance. Importantly, although small-seeded species have a higher RGR than large-seeded species at the beginning of the growth (due to their smaller initial biomass), they can never exceed the biomass of large-seeded species. This growth dynamics leads to a positive correlation between seed mass and adult mass. Hence, our model applies to communities in which species co-vary in their seed and adult biomass (see also Falster, Moles & Westoby 2008; Venable & Rees 2009; Aarssen 2015).

**Between-community variation**

Empirical studies of seed mass variation in grasslands have mostly focused on the effects of resource availability and disturbance (Pakeman et al. 2008; Metz et al. 2010; Pakeman, Lennon & Brooker 2011; Douma et al. 2012; Carmona et al. 2015; Lhotsky et al. 2016). We have therefore concentrated on these two factors in our analyses of between-community variation.
A model for seed mass variation

**Effect of resource availability**

According to our model, increasing resource availability increases the relative fitness of large-seeded species, thereby increasing CWM seed mass. This prediction is consistent with empirically observed responses of seed mass to gradients of nutrient availability (Fernandez Ales, Laffarga & Ortega 1993; Manning, Houston & Evans 2009; Bernard-Verdier *et al.* 2012; Santini *et al.* 2017). However, seed mass responses to gradients of water availability are more variable, ranging from positive (Harel, Holzapfel & Sternberg 2011; May *et al.* 2013) to neutral (Pakeman *et al.* 2008; Carmona *et al.* 2015) and even negative (Marteinsdottir & Eriksson 2014). A possible mechanism that may lead to differences in seed mass responses to nutrient vs. soil water gradients is higher tolerance of large-seeded species to low levels of water availability following germination through faster root development (Baker 1972). This mechanism can be easily incorporated in our modelling framework by adding a parameter expressing size-dependent survival to the fitness expression in Eq. 6. As expected, such extension reduces the magnitude of decrease in CWM seed mass towards low levels of resource availability, and may even lead to an increase in CWM seed mass at low resource levels (Fig. S2). Such a U-shaped response has been proposed in a recent conceptual model (Bergholz *et al.* 2015), but to the best of our knowledge, has never been observed in natural communities.

It should also be noted that the prediction of increasing seed mass with increasing resource availability is based on the assumption that soil resources are exploited size-symmetrically. While this assumption is a reasonable approximation for nutrients (Schwinning & Weiner 1998), there are reasons to believe that in some cases, competition for water might be asymmetric (e.g. due to an increase in water
A model for seed mass variation availability with soil depth). Such asymmetry can be easily incorporated in our model but currently there is no empirical evidence that justifies such extension.

Effects of disturbance

In contrast to the highly contingent response of seed mass to resource availability, disturbance (biomass removal) always increases the relative fitness of small-seeded species (Figs. 4, 5), leading to a negative correlation between disturbance intensity and CWM seed mass (Fig. 6a). Empirical studies are highly consistent with these predictions (Fernandez Ales, Laffarga & Ortega 1993; Kahmen, Poschlod & Schreiber 2002; Louault et al. 2005; Peco et al. 2005; Pakeman et al. 2008; but see Niu et al. 2010). However, little is known about the actual mechanisms that determine the advantage of small-seeded species under disturbance. According to our model, this advantage originates from a combination of three different mechanisms. First, disturbance reduces the net growth rate of all species, but this effect is more detrimental for large-seeded species due to their lower growth rate under allometric growth. Second, disturbance reduces light limitation which is stronger for small-seeded species. Third, size-dependent disturbance is more detrimental to large-seeded species due to their larger biomass. Evaluating the relative importance of these three mechanisms (growth allometry, light asymmetry, and size-dependency) in real communities is not trivial because all of them operate simultaneously in the same direction.

Notably, an advantage of small seed size under disturbed habitat conditions is also predicted by classical theories of r-K selection (Pianka 1970) and C-S-R strategies (Grime 1979). However, there is a fundamental difference between our model and previous theories: classical theories assume explicitly or implicitly that small-seeded species have an inherently higher per-capita population growth rate ($r_{max}$), and that the
A model for seed mass variation

The main advantage of small-seeded species over large-seeded ones is their ability to colonize a larger number of sites. In contrast, in our model, the advantage of small-seeded species relates to their higher biomass growth rate (RGR), which allows them to reach a higher adult mass/seed mass ratio (and therefore higher fitness) than large-seeded species. We believe that both mechanisms contribute to the advantage of small-seeded species in disturbed habitats, but their relative importance depends on the disturbance regime. A higher colonization advantage is mostly expected when disturbances are patchy and create open gaps within the vegetation cover. In contrast, advantage due to higher biomass growth rate is expected under more uniform disturbances that do not completely eliminate competition (e.g. grazing and mowing).

Interactions between the effects of resource availability and disturbance

One of the strongest results of our model is the predicted interaction between the effects of resource availability and disturbance on seed mass variation. This interaction is expressed in the effects of the two factors on the relative fitness of large-seeded vs. small-seeded species (Fig. 5), on CWM seed mass (Fig. 6a), and on the magnitude of fitness differences among species in the community (Fig. 6b).

According to our model, the degree to which increasing resource availability facilitates the relative fitness of large-seeded species decreases with increasing disturbance intensity (Fig. 5). This interaction reflects the fact that the advantage of large-seeded species in our model originates from light asymmetry. Biomass removal reduces light limitation and therefore, reduces the competitive advantage of large-seeded species over small-seeded ones. This interaction is also reflected in the response of CWM seed mass to increasing resource availability (Fig. 6a). However, the strongest response of CWM seed mass to variation in resource availability is
A model for seed mass variation

obtained under intermediate (rather than lowest) disturbance levels due to a stronger negative effect of disturbance on CWM seed mass under low resource levels (Fig. 6a).

There is also a strong interaction between the effects of resource availability and disturbance on the magnitude of fitness differences among species in the community (Fig. 6b). Two aspects of this interaction should be noted. First, moderate disturbance increases the magnitude of fitness differences under low resource levels but decreases the magnitude of such differences under high resource levels (Fig. 6b). This result provides a possible mechanistic explanation for the ‘grazing reversal hypothesis’ (the tendency of grazing to reduce species diversity under low resource levels but to increase diversity under high resource levels, Proulx & Mazumder 1998) since small fitness differences increase, while large differences decrease the likelihood of species coexistence (Kraft, Godoy & Levine 2015). This conclusion is further supported by the strong reduction in CWM seed mass under low resource levels (Fig. 6a), which indicates that disturbance acts as a strong filtering mechanism under such conditions. In contrast, under high resource levels, disturbance acts as an equalizing mechanism that promotes coexistence of large- and small-seeded species.

The second aspect of interaction concerns the response of fitness differences to variation in resource availability. According to our model, at the absence of disturbance, these differences are minimized (i.e. fitness equivalence is maximized) under intermediate levels of resource availability. This result provides a possible explanation for the well-recognized hump-shaped response of species diversity to productivity (Grace 1999; Fraser et al. 2015).

Limitations of the model

Patterns of seed mass variation are influenced by numerous processes and no model is capable of simultaneously capturing all of these processes. In this study we focus on
A model for seed mass variation

only two processes: biomass growth (as influenced by resource availability and competition) and biomass removal (as influenced by disturbance characteristics). We therefore incorporated in the model what we considered as the most fundamental elements of growth, competition, and disturbance, and ignored many other processes by which differences in seed mass may influence the performance of individual plants (e.g. seed dispersal [Greene & Johnson 1993], dormancy [Thompson 1987], emergence probability [Ben-Hur et al. 2013]) and seed predation [Tilman 1988]). Any of these processes may influence the relative fitness of large- vs. small-seeded species, thereby leading to deviations from the predictions of our model.

In addition, it should be noted that our model is not a fully demographic model. Of the three basic processes of population dynamics (reproduction, mortality, and migration), it only deals with the former process (per-capita seed production). Moreover, for a given species, the only variables that influence per-capita seed production are biomass growth and biomass removal. All other growth characteristics (e.g. root/shoot biomass allocation) are assumed to be constant in the model. Still, as demonstrated by the results, even under these restricted conditions the mechanisms affecting the performance of large- vs. small-seeded species are far from being simple and involve complex interactions between properties of the plants, the growth process, the competitive interactions, and the environment.

Finally, it should be noted that our model ignores the fact that seed mass is often correlated (positively or negatively) with other traits that influence individual fitness. Taking into account such trait-trait constraints (Douma et al. 2012; Santini et al. 2017) is a major challenge for future studies of functional trait variation.
A model for seed mass variation

Relevance for trait based ecology

Several recent studies have called for a ‘trait based ecology’, a conceptual framework focusing on traits rather than species, assuming that such approach may allow better comparisons, generalizations and testable predictions in plant ecology (McGill et al. 2006; Shipley et al. 2016). One aspect of this development is the classification of traits according to their function as stabilizing vs. equalizing mechanisms (Kraft, Godoy & Levine 2015). Most previous models of seed mass variation attempted to explain the coexistence of large- and small-seeded species and therefore focused on stabilizing mechanisms such as competition-colonization trade-off (Levine & Rees 2002) or small scale heterogeneity (Muller-Landau 2010). In contrast, the key forces incorporated in our model operate as equalizing mechanisms. Ideally, a general framework for understanding the ecological significance of seed mass variation should take into account the combined effects of both stabilizing and equalizing mechanisms.

The recent development of ‘trait-based ecology’ has also stimulated a growing number of studies that incorporate measurements of seed mass (among other key functional traits) in analyses of community structure (e.g. Pakeman et al. 2008; Bernard-Verdier et al. 2012; Diaz et al. 2016). However, currently such studies lack a mechanistic theory for interpreting their results (Adler et al. 2013; Kraft, Godoy & Levine 2015). Our model can be considered as one step towards reducing this gap. Although seed mass is only one of many important traits, results from numerous studies show that it is an important determinant of plant fitness, particularly in annual communities (Venable & Brown 1988; Levine & Rees 2002; Turnbull et al. 2004; Kraft, Godoy & Levine 2015). It also has the advantage of being ‘soft’ (easy to measure), ‘hard’
A model for seed mass variation

(important), and robust to plasticity due to environmental factors (Weiher et al. 1999).
Moreover, our findings that seed mass, growth allometry, and size-asymmetry have a crucial role in determining individual fitness through their effects on adult size are fully consistent with a recent global-scale analysis indicating that plant size is a key component of the worldwide distribution of plant functional traits (Diaz et al. 2016).
We therefore believe that these three elements (seed mass, growth allometry, and size-asymmetry) should be an integral part of any future theory of trait based ecology.

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AUTHORS’ CONTRIBUTIONS

N.D. designed the research and performed the simulations. Both authors wrote the paper.
A model for seed mass variation

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A model for seed mass variation

Table 1: Parameters common to all simulations. We used similar units ('Abstract Resource Units', ARU) for both soil resources and light, in order to simplify the construction and interpretation of the model.

| Symbol | Description (units)                        | Value |
|--------|--------------------------------------------|-------|
| $\mu$  | Maximal relative growth rate (fraction)    | 0.05  |
| $c$    | Coefficient of maintenance (ARU/mass)      | 3     |
| $k$    | Half saturation growth constant (ARU/mass) | 1     |
| $R_{\text{light}}$ | Light availability (supply rate) (ARU) | 150   |
| $\alpha$ | Reproductive allocation (fraction) | 1     |
| $t$    | Simulation length (time steps)             | 1,000 |
A model for seed mass variation

**Figure 1**: An illustration of how model results are presented. The two curves represent ‘fitness-seed mass relationships’ of two simulated communities (i and j) that differ in the value of some parameter (e.g. disturbance intensity) that influences the distribution of relative fitness among species in the community. Each fitness-seed mass relationship is characterized by its optimum (the level of seed mass that maximizes relative fitness) and the relative fitness of the most fitted species (which is equivalent to the Berger-Parker Index of dominance (BPI)).
A model for seed mass variation

Figure 2: Fitness-seed mass relationships under different levels of light asymmetry ($\theta_{\text{light}}$) and growth allometry ($a$). Other parameters: $D = 0, \bar{R}_{\text{soil}} = 100$. 
A model for seed mass variation

Figure 3: Fitness-seed mass relationships under different levels of resource availability ($\bar{R}_{soil}$), light asymmetry ($\theta_{light}$) and growth allometry ($a$).
A model for seed mass variation

**Figure 4**: Fitness-seed mass relationships under different levels of disturbance intensity \((D)\) and size-dependency \((b)\). In the left panel disturbance intensity varies while its size-dependency is constant \((b = 1.05)\). In the right panel the size-dependency varies while disturbance intensity is constant \((D = 0.01)\). Other parameters: \(a = 0.75, \theta_{light} = 1.3, R_{soil} = 100\).
A model for seed mass variation

**Figure 5:** Fitness-seed mass relationships as affected by interactions between resource availability ($\bar{R}$) and disturbance intensity ($D$). Other parameters: $a = 0.75$, $\theta_{light} = 1.3$, $\bar{R}_{soil} = 100$, $b = 1.05$. 

[Diagram showing relative fitness against log$_{10}$ Seed mass for different values of $D$: $D = 0$, $D = 0.01$, $D = 0.02$. Lines represent different resource availability ($\bar{R}$) levels: $\bar{R} = 50$, $\bar{R} = 100$, $\bar{R} = 150$, $\bar{R} = 250$.]}
A model for seed mass variation

Figure 6: Effects of resource availability ($\bar{R}_{soil}$) and disturbance intensity ($D$) on community weighted mean of log seed mass (CWM) and the magnitude of fitness differences among species in the community (quantified by the Berger-Parker Index, BPI). Other parameters: $a = 0.75$, $\theta_{\text{light}} = 1.3$, $b = 1.05$. 
A model for seed mass variation

SUPPORTING INFORMATION

Appendix S1. A comparison of fitness definitions

Most theoretical studies on seed mass variation use the classical definition of individual fitness given by Smith & Fertwell (1974) (hereafter S&F). S&F assumed that adult fitness \( W_p \) is a function of offspring fitness \( W_y \) multiplied by the number of offspring \( N \):

\[
W_p = W_y \cdot N
\]

They further assumed that the number of offspring produced by the parent \( N \) equals the ratio between the total energy invested in offspring production and that invested in an individual offspring \( (I_p / I_y \text{ in their terminology}) \). Accordingly, their definition of fitness is:

\[
W_p = W_y \frac{I_p}{I_y}
\]

When dealing with plants, the number of offspring equals the number of seeds produced per plant, and this number equals the ratio between the total biomass allocated to seed production and seed biomass \( (S_{\text{adult}} / S_{\text{seed}} \text{ in our model}) \). If differences in offspring number are the only source of fitness differences among species (i.e., no further mortality) and reproductive allocation \( (\alpha) \) is constant, S&F definition of fitness (equation 2) becomes:

\[
W_p = \alpha \frac{S_{\text{adult}}}{S_{\text{seed}}}
\]

which is exactly equation (6) in our model. However, while S&F used absolute terms of fitness, we use relative terms (see equation 7 in the main text) in order to compare
A model for seed mass variation
different simulations. Furthermore, in appendix S2 we relax the assumption that the
only source of differences in fitness is differences in offspring number by introducing
further mortality that depends on seed mass.

References

Smith, C.C. & Fretwell, S.D. (1974) The optimal balance between size and number of
offsprings. American Naturalist, 108, 499-506
A model for seed mass variation

**Appendix S2. Incorporating size dependent survival probability**

In this section we test how the predictions of the model are affected by incorporating the assumption that high seed mass increases survival probability under low resource levels. To this end, we added to equation 6 in the main text (the fitness expression) a density independent modifier of survival probability that depends on resource availability (marked in grey):

\[
O_i = \alpha_i \cdot \frac{S_i(\text{end})}{S_i(0)} \cdot \frac{\bar{R}_{soil}}{S_i(0) + \bar{R}_{soil}}
\]

In this expression survival probability increases monotonically with increasing resource availability ($\bar{R}_{soil}$), approaching one at infinite resource level. The main difference among species is in the rate by which survival probability increases with increasing resource availability which is a function of seed mass ($S_{i0}$) and an allometric survival coefficient ($\Omega$). When $\Omega$ is zero, survival probability is size invariant (Fig. S1a). As $\Omega$ decreases (becomes more negative), survival probability becomes more sensitive to seed mass (Fig. S1b, c). Importantly, since the results of the model are interpreted in terms of relative fitness, only survival probabilities that vary among species affect the model predictions.

In accordance with our model, size independent survival ($\Omega = 0$) results in a shift from small seeded species to large seeded species (i.e. an increase in CWM seed mass) with increasing resource availability (Fig. S2). Introducing size dependent survival probability increases CWM seed mass under low resource levels, and may even shift the pattern into a U-shaped relationship (Fig. S2).
Fig. S1: The dependency of survival probability on seed mass ($S_0$), resource availability ($\bar{R}_{soil}$) and the allometric survival coefficient ($\Omega$) as derived from the equation S1.
A model for seed mass variation

Fig. S2: Effects of resource availability ($\bar{R}_{soil}$) on CWM seed mass under different values of the allometric survival coefficient ($\Omega$). Other parameters: $a = 0.75$, $\theta_{light} = 1.3$, $D = 0$. 