LETTER

Why equalising trade-offs aren't always neutral

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Abstract

Equalising trade-offs, such as seed mass vs. number, have been invoked to reconcile neutral theory with observed differences between species. This is an appealing explanation for the dramatic seed size variation seen within guilds of otherwise similar plants: under size-symmetric competition, where resource capture is proportional to mass, the outcome of competition should be insensitive to whether species produce many small seeds or few large ones. However, under this assumption, stochastic variation in seed rain leads to exclusion of all but the smallest-seeded species. Thus stochasticity in seed arrivals, a process that was previously thought to generate drift, instead results in deterministic competitive exclusion. A neutral outcome is possible under one special case of a more general equalising framework, where seed mass affects survival but not competition. Further exploration of the feasibility of neutral trade-offs is needed to understand the respective roles of neutrality and niche structure in community dynamics.

Keywords

Demographic stochasticity, Jensen's inequality, life-history trade-offs, lottery models, neutral theory, pioneer trees, seed mass, seed size, spatial variance, stochastic dispersal.

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INTRODUCTION

Strict neutrality demands absolute equivalence between individuals of different species (Hubbell 2001). However, because this assumption seems so obviously wrong, theory employing strict neutrality is rather unpalatable to many ecologists (Zhang & Lin 1997; Yu *et al.* 1998; Adler 2004). After all, co-occurring species differ in many ways: for example, forest trees produce seeds of different sizes (Lord *et al.* 1995), grow at different rates (Pacala *et al.* 1996; Wright 2002), and have different typical life-spans (Kobe *et al.* 1995). To accommodate these differences within a neutral framework, individuals belonging to species with different characteristics must have equal per-capita fitness (Bell 2001; Hubbell 2001; Chave 2004). This might be possible if life-history traits are constrained by a series of precise, equalising trade-offs (Hubbell 2001) such that all combinations of traits have equal fitness.

However, because even small differences in fitness quickly lead to exclusion, such equalising trade-offs must be perfectly compensating (Zhang & Lin 1997; Yu *et al.* 1998); leading Chesson to emphasise the importance of

stabilising mechanisms (Chesson 2000; Adler *et al.* 2007). While the ecological literature is replete with potential stabilising mechanisms, most ecologists would probably be hard-pressed to identify possible equalising mechanisms. However, one suitable candidate for an equalising trade-off is a competition/fecundity trade-off. For a given reproductive mass M, the fecundity is M/S, where S is seed mass, so a plant can either produce many small seeds or a few large ones (Smith & Fretwell 1974). But, if the subsequent competitive ability of the seedlings is proportional to the initial mass S (i.e. competition is size-symmetric) then the combined fitness of the seedlings ($M/S \times S$) is independent of S; in which case, seed mass should be free to drift (Dalling & Hubbell 2002). This might help to explain why co-occurring species in the same guild show orders of magnitude variation in their seed masses (Rees 1995; Moles *et al.* 2005).

Surprisingly, although several more complex, stabilising versions of the competition/fecundity trade-off have been examined previously (Geritz 1995; Rees & Westoby 1997) an equalising version has been proposed but never fully explored (Dalling & Hubbell 2002; Cadotte 2007). Here, we

show that even when the trade-off is equalising, random variation in the initial number of seeds colonising a site generates an advantage to small-seeded species. This is due to a spatial variance mechanism, in which small-seeded species benefit by distributing biomass more evenly. We show that this seemingly trivial difference can cause rapid competitive exclusion of large-seeded species in models parameterised with field data.

METHODS AND RESULTS

In the models presented here seeds that fall into suitable patches compete for available resources and, because of the seed mass/number trade-off, the number of seeds arriving in each patch, n_i, is inversely related to the mass of individual seeds, S_i. We build in neutrality by assuming that competition is perfectly size-symmetric, such that

$$P_i = \frac{n_i S_i}{\sum_j n_j S_j} \qquad (1)$$

where P_i is either the proportion of resources obtained from a patch, or the probability of capturing an entire patch. That is, a given mass of seeds obtains the same proportion of the total resources, independent of whether this mass is composed of many small seeds or a few large ones. Thus, we expect that species will have equal fitness independent of their seed mass and that neutral dynamics will emerge, i.e. although we might expect to see stochastic extinctions, we expect no general correlation between seed mass and extinction risk.

We first outline a simple analytical approximation in which the seeds of two species fall into patches and compete for resources according to eqn 1. This analytical result demonstrates that there is an advantage to smaller seeds due to a spatial variance mechanism. To determine whether such an advantage would have any impact in real communities, we present two simulation models with parameters taken from field observations. The first model is appropriate for annuals living in a matrix of perennials where species tend to have different adult sizes (as well as different seed sizes), and the second is a more traditional lottery model, with equally-sized adults, appropriate for forest trees.

A simple analytical approximation

For each species i, we assume that after seed dispersal, a number of seeds, $n_{i,q}$ of individual mass S_i, fall into each patch or gap, q. Thus, the total mass of seeds, $T_{i,q}$ dispersed into each patch is, $T_{i,q} = S_i n_{i,q}$ and

$$E\{T_i\} = S_i E\{n_i\} \qquad (2)$$

where $E\{\}$ indicates the expectation or average. We can then use the fact that $\mathrm{var}(aX) = a^2.\mathrm{var}(X)$ to see that the variance across patches in the total mass of seeds, T_i is,

$$\mathrm{var}(T_i) = \mathrm{var}(S_i n_{i,q}) = S_i^2.\mathrm{var}(n_{i,q}) \qquad (3)$$

Under Poisson dispersal, $\mathrm{var}(n_{i,q}) = E\{n_{i,q}\} = \bar{n}_i$ and therefore

$$\mathrm{var}(T_i) = S_i^2.\bar{n}_i \qquad (4)$$

Substituting $\bar{n}_i = E\{T_i\}/S_i$ into eqn 4 gives $\mathrm{var}(T_i) = E\{T_i\}S_i$. That is, the patch-to-patch variance in the total mass of seeds is proportional to seed mass. This has profound consequences, because, when competition is for finite resources, the relationship between the total mass of seeds and resource (or gap) capture is non-linear, such that the variance biases the mean fitness.

To see why, we consider two species with different seed masses which occupy a system of patches: one species (*large*) produces very large seeds (of mass S_l) and the other (*small*) produces very small seeds (of mass S_s). After one generation of seed production and Poisson dispersal, the patch-to-patch variance in the total mass of *small* seeds is approximately zero. In contrast the patch-to-patch variation in the total mass of *large* seeds is substantial. Therefore, we can approximation the dynamics by assuming that *small* contributes a constant total mass of seeds T_s to all patches. Assuming perfectly size-symmetric competition (eqn 1) the average resources captured by *large* (B_l) will then be

$$E\{B_l\} = E\left\{ R\left(\frac{n_{l,q} S_l}{n_{l,q} S_l + T_s} \right) \right\}, \qquad (5)$$

where R is the resources available per patch, S_l is the seed mass of *large* and $n_{l,q}$ is the number of *large* seeds per patch. By Taylor expanding around the mean ($\bar{n}_l$) and taking expectations, we find

$$E\{B_l\} \approx R\left[\frac{\bar{n}_l S_l}{T_s + \bar{n}_l S_l} - \frac{T_s S_l^2 \sigma_l^2}{(T_s + \bar{n}_l S_l)^3} \right], \qquad (6)$$

where σ_l^2 is the variance in the number of *large* seeds per patch. Note that the spatial variation in the number of *large* seeds reduces the average resources captured by *large*. In contrast, the average resources captured by *small* (B_s) in a patch will be

$$E\{B_s\} \approx R\left[\frac{T_s}{T_s + \bar{n}_l S_l} + \frac{T_s S_l^2 \sigma_l^2}{(T_s + \bar{n}_l S_l)^3} \right]. \qquad (7)$$

Crucially, the same spatial variance that reduces the resources captured by *large* (the second term in square brackets) actually benefits *small*. This shows that the advantage to small-seeded species occurs because (1) there is higher spatial variation in the total mass of seeds per patch

for large-seeded species, and, (2) competition is non-linear and so the patch-to-patch variance in total seed mass affects average fitness: an example of Jensen's inequality (Ruel & Ayres 1999).

At an intuitive level, the non-linearity arises because the resources available in each patch are capped by the environment. This introduces diminishing returns; such that, with substantial variation in the number of seeds arriving, the additional resources captured in patches which receive extra seeds cannot compensate for the resources lost in patches which receive few seeds. Thus, it is never better to increase the chance of capturing any particular patch at the expense of reducing the chance of capturing resources elsewhere. The optimum strategy in this case is to equalise the chances of capturing resources from all patches, and this is exactly what small-seeded species do.

Annual plants

As a specific example, we begin with a model appropriate for annual plants living within a matrix of perennials, e.g. European sand-dune annuals. In these communities, suitable habitat for annuals typically consists of gaps in this matrix (Watkinson *et al.* 2000). We consider a total area of dune A (m^2), a fraction H of which consists of habitat suitable for annuals (hereafter patches). All patches have area a (m^2), giving a number of suitable patches $N = HA/a$. At the start of each year t, a number of seeds $n_{i,q,t}$ of each of the j annual species falls into each patch q. These seeds then grow into plants giving, for each species i, an end-of-season biomass for each patch, $B_{i,q,t}$, which can be summed over the whole area to yield, $B_{i,t}^{tot} = \sum_q B_{i,q,t}$. We assume that patches can produce a maximum biomass of adult plants per unit area K (g m^{-2}), and that seeds grow exponentially until the combined mass of all individuals within the patch reaches the limit aK (g), after which there is no further growth. We assume that the growth period, t, is the same for all annual species, so that a seed of initial mass, S_i, can reach a maximum end-of-season mass (M_i) given by

$$M_i = S_i * \exp(\beta t) \tag{8}$$

The exponential growth form is in keeping with the assumption of size symmetry, i.e. that resource capture is always proportional to mass. To simplify matters, we set $t = 1$, and choose a fixed value of β which converts a seed into an adult plant in a single time step.

If the patch limit aK is not exceeded, each seed reaches an adult biomass given by eqn 8. Otherwise, each species obtains a proportion ($P_{i,q,t}$) of aK according to its seed mass (S_i) and the number of seeds which land in that patch ($n_{i,q,t}$). Specifically, we assume that competition is perfectly size-symmetric, such that $P_{i,q,t} = n_{i,q,t} S_i / [\sum_j n_{j,q,t} S_j]$ (see eqn 1). At the end of each growing season, each individual converts

its adult biomass into new seeds, which are dispersed to give the initial condition for the next year's growth. Seeds that fall into the perennial matrix are lost. We begin by assuming uniform dispersal. In this case the average seed rain into the patches $\bar{n}_{i,t}$ (which is also the expectation for the seed rain into any given patch q, denoted $E\{n_{i,q,t}\}$) is given by

$$\bar{n}_{i,t} = E\{n_{i,q,t}\} = \frac{HB_{i,t-1}^{tot}}{S_i N} \tag{9}$$

(i.e., the fraction H of seeds that are not lost to the matrix are shared equally among the N patches).

In this case, each patch is identical so we only need to consider the outcome of competition in a single example patch, q and then multiply this up to the community scale. The total biomass of all annuals combined at the end of each growing season, $\sum_j B_{j,q}$ is equal to aK (for simplicity we will assume all resources are used) and therefore we can write the dynamics of the biomass for each species as:

$$
\begin{aligned}
B_{i,q,t+1} = aKP_{i,q,t+1} &= aK\left(\frac{E\{n_{i,q,t+1}\}S_i}{\sum_j E\{n_{j,q,t+1}\}S_j}\right) \\
&= aK\left(\frac{(B_{i,q,t}/S_i)H(1/N)S_i}{\sum_j (B_{j,q,t}/S_j)H(1/N)S_j}\right) \\
&= aK\left(\frac{B_{i,q,t}}{\sum_j B_{j,q}}\right) = aK\left(\frac{B_{i,q,t}}{aK}\right) = B_{i,q,t}
\end{aligned}
\tag{10}
$$

where q denotes an example patch. Note that, the biomass of each species in each patch remains the same from one year to the next, regardless of the mix of seed masses present in the community. Equation 10 can be re-written in terms of the individual plants in the community, rather than species (not shown). This shows that each plant contributes its own final biomass in year t, to the final biomass in year $t+1$, even if it mutates to produce a seed mass different from the mass of the seed from which it grew. Clearly, in every sense, the dynamics of this special case are neutral.

However, in reality the seed input into any given patch must be subject to randomness, leading to variation in seed input among patches. We incorporate this into the model in the simplest way: we make the seed input $n_{i,q,t}$ to each patch q a random number, drawn from a Poisson distribution with mean $\bar{n}_{i,t}$. The Poisson distribution is used here as we are assuming that seeds are dispersed across the entire habitat, so the model does not include any intraspecific aggregation of seeds that might result from local dispersal. We also draw the $n_{i,q,t}$ independently for each species; so the model does not include any interspecific aggregation or segregation of seeds (Turnbull *et al.* 2004, 2007).

We simulated the model using seed masses from a community of nine European sand-dune annual species (0.006 g to 2.924 mg) that have been intensively studied

(Mack & Harper 1977; Rees *et al.* 1996; Turnbull *et al.* 2004, 2007, 2008). We fixed the total area of suitable habitat to 10% (again, in line with field measurements; Turnbull 1998), and began with each species having an equal fraction of the total available biomass. With Poisson seed rain, neutral dynamics are only achieved when the suitable habitat is available as a single very large patch and the spatial variance mechanism does not operate (Fig. 1a and b). Otherwise, with patch sizes set to a realistic value (Turnbull 1998), the species with the smallest seeds clearly has the highest fitness, driving larger-seeded species to extinction (Fig. 1c and d).

The greater the subdivision of the suitable habitat, the greater the fitness differences, so that when the suitable habitat is subdivided into 2000 patches, the species with the largest seeds persists for less than 1000 generations (Fig. 1e and f). Notice that, because large-seeded species have lower population sizes, the same result might be obtained simply through demographic stochasticity. To test the importance of this, we implemented the model with the same number of species, all with seed mass equivalent to the largest species. No extinctions were observed (Fig. S2, supporting information). Thus, with these parameters, it is the spatial
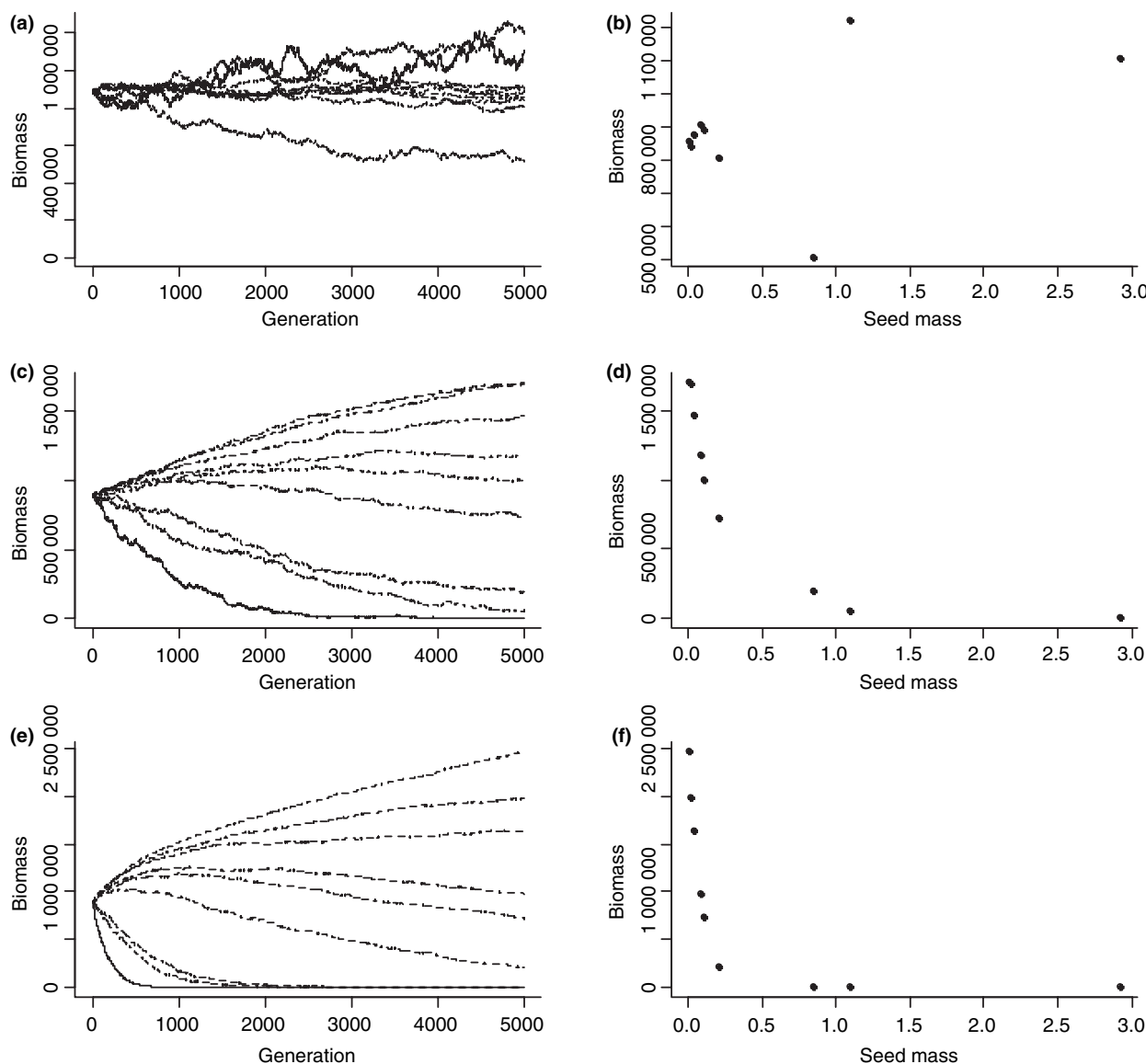
Figure 1 Trajectories and final biomasses of a guild of nine sand-dune annual species in the annual plant model when dispersal is global and competition is perfectly size-symmetric. The suitable habitat consists of only 10% of the total area and is available either as a single patch (a & b), 500 patches (c & d) or 2000 patches (e & f).

variance mechanism, and not demographic stochasticity that leads to the exclusion of large-seeded species. The introduction of local dispersal and patch-level disturbance does not alter the conclusions presented here (Appendix S1 & Fig. S3).

In eqn 1, there is no effect of seed mass on survival of seeds or seedlings. However, more generally we could write

$$P_i = \frac{n_i E_i C_i}{\sum_j n_j E_j C_j}, \qquad (11)$$

where E_i is the probability that a seed or seedling survives to the point of germination and C_i is its subsequent competitive ability. Neutrality could be introduced into this more general formulation by assuming that $E_i \propto S_i^\alpha$ and $C_i \propto S_i^{1-\alpha}$, although we note that there is no biological reason why these functions should be constrained in this way. In this case, the advantage to producing large seeds lies partly in increasing the chances that each seed germinates and survives, and partly in their enhanced ability to capture limiting resources. For all values of α, other than the special case where $\alpha = 1$, this more general formulation behaves in the same way as before, with competitive exclusion of all but the smallest seeded species. That is, the spatial variance mechanism outlined above generates an advantage to smaller seeds except in the special case of $\alpha = 1$, when competitive ability is completely unrelated to seed size (Fig. S1). In this case, the model becomes truly neutral: small-seeded species produce more seeds but this is exactly balanced by their poor survival. Thus, all species end up with exactly the same average number of seeds, which now compete on equal terms, despite their size differences.

Forests

Hubbell's neutral model (Hubbell 2001) was devised with tropical rainforests in mind. The model assumes a community with a fixed number of sites, N, each occupied by a single canopy tree of species i (but see Etienne *et al.* 2007); hence the number of sites, N is also the number of individuals. Each site (and hence each canopy tree) has identical area, a and is subject to a probability, D of being disturbed in a given time interval. Disturbance means that the adult is removed, after which the site is captured by a new canopy tree, the species of which is determined by drawing randomly, according to the species composition of the community as a whole. The lottery in this case occurs between the seeds which fall into each gap following disturbance: a probability of gap capture $P_{i,q,t}$ is assigned for each species i with respect to site q disturbed at time t. In keeping with the idea that competition is size-symmetric, we assume

$$P_{i,q,t} = \frac{n_{i,q,t} S_i}{\sum_j n_{j,q,t} S_j}, \qquad (12)$$

where $n_{i,q,t}$ is the number of seeds of species i in site q at time t. Note the similarity with eqn 1, which was defined for the annual plant model: the difference is that in the forest model, $P_{i,q,t}$ represents a probability of complete capture of site q, whereas in the annual plant model, $P_{i,q,t}$ represented the proportion of resources of patch q assigned to species i (Chesson & Warner 1981; Geritz *et al.* 1999). Notice that (1) this is just a weighted lottery, with the weightings determined by the seed masses; (2) the probability that species i captures the site depends on the total seed mass of species i in the site, irrespective of whether this seed mass is divided into a few large, or many small, seeds.

To calculate the seed input into each site, we assume that canopy trees of all species produce an equal biomass of seeds per unit time, M. In this case, species producing large seeds will inevitably produce fewer seeds per canopy tree per year, according to the simple trade-off: $\tilde{n}_i = M/S_i$ where $\tilde{n}_i$ is the number of seeds per year produced by a canopy tree of species i and S_i the seed mass (Henery & Westoby 2001). We begin by assuming uniform dispersal, giving: $\bar{n}_{i,t} = E\{n_{i,q,t}\} = (\tilde{n}_i N_{i,t})/N$, where $\bar{n}_{i,t}$ is the average or expected seed input into each patch. As in the annual plant model this special case generates neutral dynamics: in fact, it simply recreates Hubbell's original formulation:

$$P_{i,q,t} = \frac{E\{n_{i,q,t+1}\} S_i}{\sum_j E\{n_{j,q,t+1}\} S_j} = \frac{(M/S_i) S_i N_{i,t}}{\sum_j (M/S_j) S_j N_{i,t}} = \frac{N_{i,t}}{N} \qquad (13)$$

i.e. the probability that species i captures an available site is equal to the proportion of the canopy trees in the community consisting of species i at that time (see Hubbell 2001). Therefore, as was seen in the same special case for annual plants (eqn 10), on average, each species i contributes its current biomass to next year's community, independent of seed mass; and the same holds for each individual canopy tree, such that seed mass is free to change through mutation with no consequences for fitness.

As before, incorporating random (Poisson) seed dispersal destroys the neutral dynamics. For simulations, we take parameters from 14 pioneer tropical tree species intensively studied in Panama whose seed masses vary from 0.007 to 28 mg (Dalling & Hubbell 2002; the single herbaceous species was excluded and we used the average seed mass reported for the *Zanthoxylum* spp which were not identified separately in the original study). These particular species appear to fulfil the requirements for a neutral trade-off: fecundity decreases with seed mass across species, while recruitment probability on a per-seed basis increases with seed mass (Dalling & Hubbell 2002; Figure 3). Normally, the pioneer guild occurs within a forest dominated by shade tolerators, which are longer-lived (Clark & Clark 1992). To represent this, we included a single shade tolerator species,

with a disturbance rate D compared to $r.D$ for the pioneers. When a shade-tolerator dies, the site is immediately occupied by one of the pioneer species, following a lottery using the rule given in eqn 12; and when a pioneer dies, the site is immediately occupied by the single shade-tolerator species, and hence unavailable to pioneers until the shade-tolerator individual dies. The dynamics of shade-tolerators and pioneers then follows a 2-state Markov chain, and the equilibrium proportion of sites occupied by shade-tolerators is $r/(1 + r)$. We chose $D = 1/150$ years and, $r = 3$, so that, on average 75% of the canopy trees are shade-tolerators which live for an average of 150 years, while the other 25% consists of pioneers that live on average for 50 years (Clark & Clark 1992).

One unknown but important quantity is the average number of seeds competing for each gap. In reality this depends on many factors including the fecundity of adult trees and the frequency with which they produce seeds, rates of seed predation and the survival of seeds in the soil seed bank. However, to simplify the situation, we can set the fecundity of adult trees so that the number of seeds arriving per gap in the model matches that observed in typical gaps of 100 m². Dalling & Hubbell (2002) recorded the number of pioneer seedlings which emerge following the creation of artificial gaps. They found roughly 40 seedlings m⁻²; hence

4000 seedlings per gap and 10 000 seedlings per gap once the litter was removed. These numbers probably reflect the number of viable seeds which can contend for the site, although the total number of buried seeds in the top 6 cm of soil is even higher (roughly 1000 m⁻²).

We simulate different cases to see the effect of introducing random variation in the number of seeds arriving in each gap and the effect of increasing total fecundity, on competitive outcomes. First, we compare simulations in which initial numbers of seeds in each gap are always equal to the expectation (see eqn 13: we expect this case to have neutral dynamics), with simulations in which initial numbers of seeds are drawn from a Poisson distribution. Second, we change the average number of viable seeds which take part in the lottery for each gap by setting the fecundity of adult trees to give on average 2000, 7000 or 30 000 seeds competing for each gap. In each case we simulate a forest consisting of 10 000 trees for 10 000 years. Because there was greater stochasticity between runs than in the annual plant model, we simulate each case 1000 times and take the average population size of each species.

When each site receives the expected seed rain, the model exhibits neutral dynamics (Fig. 2a). However, with Poisson seed rain, and 2000 viable seeds per gap, the seven species
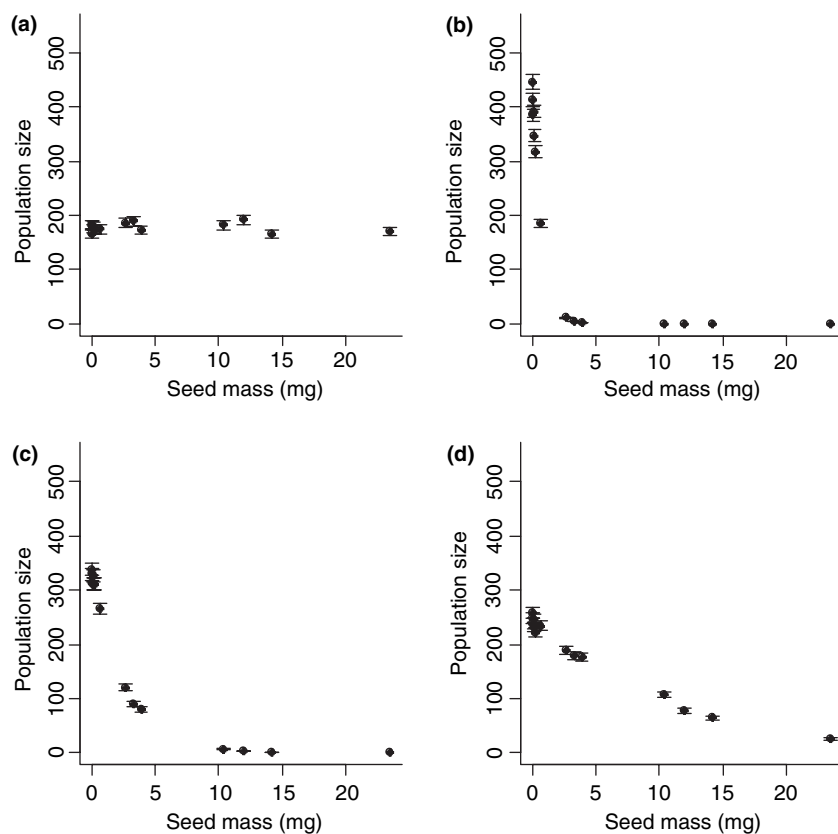
Figure 2 The effect of seed mass on average final biomass for a guild of 14 tropical pioneer trees in the forest model when each gap receives exactly the expected seed rain (a) or the initial seed numbers are drawn from a Poisson distribution (b–d). The total number of viable seeds which compete for each gap is either 2000 (a & b), 7000 (c) or 30 000 (d). In each case, final population size is calculated from 1000 runs each lasting 10 000 generations from a model forest containing 10 000 canopy trees.

with the largest seeds are all but extinct after 10 000 years (Fig. 2b). With 7000 viable seeds per gap, the four species with the largest seeds make up less than 1% of pioneer trees (Fig. 2c) and even with 30 000 viable seeds per gap; the species with the largest seeds is 10 times less abundant than the species with the smallest seeds after 10 000 years (Fig. 2d). Thus, increasing the total seed production makes the dynamics increasingly neutral, but true neutrality would only be achieved with infinite fecundity.

DISCUSSION

Seed mass differences spanning 3–4 orders of magnitude are almost ubiquitous among guilds of functionally similar plants with similar adult sizes (Moles *et al.* 2005). Thus, the seed mass/number trade-off in some form or other is one of the dominant life-history axes of land plants (Westoby & Wright 2006). The seed mass distributions used here are typical of plant communities generally: they are approximately log-normal with many species having small seeds and rather fewer having large seeds (Rees 1995; Davies & Ashton 1999; Guo *et al.* 2000; Dalling & Hubbell 2002; Murray *et al.* 2005). The spatial variance mechanism ensures that such large differences in seed mass are unlikely to persist under a neutral formulation unless seed mass only affects the probability of seed survival with no further effects on the ability of seedlings to capture limiting resources (the special case of $\alpha = 1$). This in turn implies that seedling growth would never be size-dependent and that competitive ability would never be correlated with size. However, for sand-dune annuals the initial growth phase is mass-dependent (Turnbull *et al.* 2008) and competitive interactions are mass-related (Mack & Harper 1977; Rees 1995; Turnbull *et al.* 2004). In addition, the special case of $\alpha = 1$ predicts no negative correlation between seed size and abundance, for which there is substantial empirical evidence from a variety of annual communities (Levine & Rees 2002; Murray *et al.* 2005).

Paradoxically, while drift dynamics are often assumed to be a natural consequence of demographic stochasticity in dispersal (Etienne & Alonso 2005, 2007), it is the inclusion of stochastic seed arrivals which destroys the neutrality in the models presented here. This occurs because the variance in the total mass of seeds dispersed into each patch is greater for large-seeded species. This generates a fitness cost whenever the payback on the investment represented by the seed is capped by the environment, and therefore the function relating total seed mass to resources captured is decelerating or concave-down. In this case, it is always better to equalise the probability of capturing resources across patches; analogous to the finding in behavioural ecology that foraging strategies that equalise effort in space are the most efficient (Adler & Gordon 2003). The problem

is magnified if average fecundity falls (for example in low productivity habitats) particularly if it falls to the point where large-seeded species completely fail to arrive at some sites. In fact under an equalising trade-off, neutrality is only restored when stochasticity in seed dispersal is removed. Notice that, neutrality cannot easily be re-instated into such models – for example, by introducing an additional arbitrary advantage to larger seeds – as the fitness differences which arise from different seed masses depend on environmental characteristics such as the number and size of patches which are unlikely to be stable across space and time.

The expected time to extinction of large-seeded species depends strongly on the number of seeds competing for each patch. Whether or not seed production is therefore high enough to give long expected times to exclusion is likely to be system dependent. For example, in sand-dune annual communities recruitment limitation is widespread among large-seeded species (Turnbull *et al.* 1999). However, trees can undoubtedly produce very large numbers of seeds and, in some cases, synchronise production of extremely large numbers of seeds over large areas (masting : Sork *et al.* 1993; Kelly 1994). Indeed, it is known that at least some species in temperate forests can blanket the forest floor with seeds (Clark *et al.* 1998). However, a neutral outcome demands not just that some species can achieve this, but that all can. In addition, dispersal kernels parameterised for species in temperate forests (e.g. Ribbens *et al.* 1994; Clark *et al.* 1998) normally reveal that small-seeded species also achieve better spatial dispersal of their seeds, magnifying the problem.

The seed competition/fecundity trade-off can be formulated in such a way that it is stabilising rather than equalising by assuming some degree of competitive asymmetry (Tilman 1994; Chesson 2000). Initially, models of competition/fecundity trade-offs, which can be explicitly formulated in terms of seed mass (Geritz 1995; Rees & Westoby 1997; Geritz *et al.* 1999), were thought to allow the coexistence of an infinite number of species (Tilman 1994). However, it is now known that this is only true when the degree of competitive asymmetry is infinite, so that species with a particular seed mass are totally unaffected by competition with any species with a lower seed mass, no matter how small the size difference (Kinzig *et al.* 1999; Levine & Rees 2002). Such infinite competitive asymmetry leads to pathological dynamics and is biologically unfeasible (Kinzig *et al.* 1999). Relaxing the assumption of extreme asymmetry can allow coexistence of a small number of species, but diversity is low (Adler & Mosquera 2000). However, if the trade-off itself is not stabilising, stabilisation can always come from other processes, such as Janzen-Connell effects (Augspurger 1983; Condit *et al.* 1992; Freckleton & Lewis 2006) or temporal or spatial storage effects (Chesson & Huntly 1997; Clark *et al.* 2004). Chesson

has repeatedly emphasised that such stabilising mechanisms are probably hard to avoid in reality and very little stabilisation is required once equalizing trade-offs have reduced fitness differences between species (Chesson 2000).

Neutrality has been fervently embraced by some ecologists and equally firmly rejected by others (Chesson & Rees 2007; Clark et al. 2007). Its supporters often point to its more general contribution to community ecology: it has provided a null model against which the effects of species differences can be assessed, stimulated debate and shown that some community-level patterns do not appear to require anything more than fitness equalisation and demographic stochasticity (Bell 2001; Chave 2004; Alonso et al. 2006). This praise is undoubtedly well-deserved. However, we believe it is wrong to invoke Occam's razor as grounds for accepting the neutral model as an adequate description of an ecological community simply because it can reproduce some well-known patterns with minimal assumptions. If the neutral model is structurally unstable to the inclusion of species differences, then we are justified in choosing a more complex model which can accommodate these differences; for example, one which includes density-dependence, and hence stabilisation (Chesson 2000; Chave et al. 2002; Volkov et al. 2005).

While no-one actually believes that species are the same, equalizing trade-offs might appear to offer a more realistic way for ecological communities to display neutral dynamics. However, models explicitly incorporating particular equalizing life-history trade-offs remain almost entirely unexplored. The results presented here show that one apparently neutral trade-off cannot be neutral in reality, because it is unstable to the inclusion of stochastic seed dispersal. Models of other putative neutral trade-offs are needed before we reach a true consensus on the respective roles of niches and neutrality in structuring ecological communities (Tilman 2004; Adler et al. 2007).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

A word document containing the following:

- **Figure S1** Results from a more general model: $P_i = n_i E_i C_i / [\sum_j n_j E_j C_j]$ where E_i is the probability that a seed or seedling survives the pre-competition stage and C_i is its subsequent competitive ability.
- **Figure S2** Model runs with nine species all with seed mass equivalent to the largest species in the annual plant guild for comparison with Fig. S1.

- **Figure S3** Typical trajectories of nine sand-dune annual species in the growth model when all seeds are dispersed globally (a,c,e) or when only 40% of seeds are dispersed globally and 60% of seeds are retained within patches (b,d,f).
- **Appendix S1** Local dispersal and disturbance.

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