

WHICH TRADE-OFF CONTRIBUTES MOST TO BIODIVERSITY? A COMPARISON OF TRADE-OFF MODELS

1. INTRODUCTION

No single species can allocate unlimited resources to each life history trait [?]. Instead, species life histories are determined by the allocation of limited resources to different areas of need. In plant species, the three most important life history traits are reproduction, growth from seedling to adult, and defence against both herbivory and abiotic factors such as fire ([?]). This leads to trade-offs between life history traits; for example, a species with high levels of resource allocated to increasing fecundity will not be able produce seeds of a large mass ([?]) and will therefore experience a decrease in its juvenile growth rate ([?]), or a species with rapid growth may be more susceptible to damage by storm winds or other mortality pressures such as large scale herbivory (e.g. [?, ?]). Theory has shown that these trade-offs can allow two or more species to coexist while competing for the same resources in an environment (e.g. [?, ?, ?]), suggesting that trade-offs are important for sustaining high levels of biodiversity in nature.

However, conditions under which species coexist alongside others will also be dependent on other, abiotic factors. Several previous studies have suggested that disturbance events also play an important role in promoting and maintaining diversity (e.g. [?, ?]). Recent theoretical work ([?]) show that different measures of disturbance, such as frequency or intensity, will have very different effects, even when the total biomass lost to disturbance over a given time period is taken into account. While many empirical studies consider disturbance as a single parameter (e.g. [?, ?, ?]), some studies do demonstrate that different factors determining disturbance can affect the community structure differently. Hall and Miller [?] use bacterial populations to demonstrate that the frequency and intensity of disturbance events have different impacts, while Denslow [?] indicates that communities with large, infrequent disturbances may be more diverse than those where disturbance events are more frequent, yet clear a smaller area (e.g. tree-fall gaps).

Here, all possible trade-offs between the three most important plant life history traits - reproduction, juvenile growth and defence - are considered. Defence is considered as the ability of an individual to withstand a disturbance event, that is, an event that results in the death of large number of individuals and alters niche opportunities within the community, while seed production (seed number per capita per year) is used as the measure of resource allocation. We therefore consider 8 models. The model where all species are identical gives neutral dynamics, and the coexistence of the two species is governed by chance, while the 3 where the species differ in a single trait (no trade-off) demonstrate competitive exclusion of the weaker species. When trade-offs are between two or more traits, the effects of system capacity and varied disturbance regimes are considered, and we show that trade-offs between fecundity and growth, or growth and defence, can support two species for large system sizes, as can a three dimensional trade-off, although a fecundity-defence trade-off cannot. The probability of species disturbance resistance parameters resulting in coexistence is calculated, and we demonstrate that a three dimensional trade-off gives the greatest likelihood of coexistence, an order of magnitude larger than that

of a growth-defence trade-off. Species specific disturbance intensities are then linked to allow comparison between the three dimensional trade-off and a fecundity-growth trade-off where disturbance affects all species equally, and we show that if the more fecund of the two species has a slight advantage in defence against disturbance, the likelihood of coexistence is maximised.

2. MODELS

Here, we build on the model presented in Chapter 2, introducing a single extra factor. Now, we allow species to differ in the level of resource they dedicate towards resistance to disturbance events, so an individual of species i will experience a species specific probability of death during a disturbance I_i . The model is described in a non disturbance time step by the following transition probabilities (where $n = N_1(t)$ and $N - n = N_2(t)$);

$$P(\text{increase}(n)) = \frac{N-n}{N} \frac{s_1 n}{s_1 n + s_2(N-n-1)} \exp\left(-s_2 \frac{N-n-1}{N} x\right), \quad (1)$$

$$P(\text{decrease}(n)) = \frac{n}{N} \frac{s_2(N-n)}{s_1(n-1) + s_2(N-n)} + \frac{n}{N} \frac{s_1(n-1)}{s_1(n-1) + s_2(N-n)} \left(1 - \exp\left(-s_2 \frac{N-n}{N} x\right)\right), \quad (2)$$

$$P(\text{stay}(n)) = 1 - P(\text{increase}(n)) - P(\text{decrease}(n)). \quad (3)$$

where s_i is the per capita annual seed production of species i , N is the system capacity - the maximum number of adults that can be sustained by the environment, and $x = C(1/g_1 - 1/g_2)/2$ is a measure of growth rate differences (with C canopy height and g_i the sapling growth rate of species i).

During a disturbance event, each individual of species i will die with probability I_i . If there are d_i deaths of species i , then the total deaths is given by $d = \sum_i d_i$. Note that d is now dependent on the species composition of the community when the disturbance strikes, as well as the inherent properties of the disturbance. The expected number of deaths is given by

$$\bar{d} = \sum_i I_i N_i(t) \quad (4)$$

where $N_i(t)$ is the population of species i at time t . Once all d deaths occur, the remaining $N - d$ individuals compete for the opened sites in the system. **If the populations of the two species are given by n_1^*, n_2^* in the immediate aftermath of a disturbance, the probability of each gaps being successfully colonised by species one is given by**

$$Sp_1(n_1^*, n_2^*) = \frac{s_1 n_1^*}{s_1 n_1^* + s_2 n_2^*} \exp\left(-s_2 x \frac{n_2^*}{N}\right). \quad (5)$$

We assess coexistence by considering invasion analysis. The average or expected change in a time step is given by

$$\text{AverageChange}(n) = (1-f)(P(\text{increase}(n)) - P(\text{decrease}(n))) + f(-nI_1 + (nI_1 + (N-n)I_2)Sp_1(n(1-I_1), (N-n)(1-I_2))). \quad (6)$$

Coexistence occurs when on average, both species increase when rare; that is when

$$\begin{aligned} \text{AverageChange}(1) &> 0, \\ \text{AverageChange}(N-1) &< 0. \end{aligned}$$

We can now consider a collection of models by varying a different combination of the three traits; fecundity, juvenile growth rate and defence or resistance to disturbance. This gives a selection of 8 models, one where the species are identical, 3 where they differ in a single parameter, 3 where they differ in two ways and the third parameter is equal, and a final model where species can differ in all three ways. The first four of these are trivial to analyse, but the models where species differ in at least two of the life history parameters give more interesting dynamics.

Table of parameters		
Parameter	Description	Default value
s_1	per capita annual seed production of species 1	500
s_2	per capita annual seed production of species 2	50
g_1	growth rate of species 1 juveniles (measured in mm/yr for diameter at breast height)	13
g_2	growth rate of species 2 juveniles (measured in mm/yr for diameter at breast height)	13.21
C	size of individuals at canopy height (measured in mm for diameter at breast height)	100
x	$C(1/g_1 - 1/g_2)/2$ time window for successful secondary colonisation by species 2	0.06
x_s	sx when $s_1 = s_2 = s$	3
N	system capacity: number of individuals the region can support	1000
n	number of species 1 individuals	N/A
T_D	average time between disturbances in yrs	10
f	within event disturbance probability	$100/(T_D N)$
I_1	intensity of disturbance for species 1	N/A
I_2	intensity of disturbance for species 2	N/A
y	Parameter linking species intensities; given by I_1/I_2	N/A

3. RESULTS

When all species are identical, the model is simply a one-dimensional random walk, where disturbance events of intensity I merely increase the distance it is possible to travel in a single step. Coexistence in this model is merely a function of chance. If the species merely differ in a single parameter, then that with the higher growth rate or fecundity, or with the lower mortality in a disturbance regime will competitively exclude the other.

3.1. Fecundity-growth trade-off. The case where species differ in both fecundity and growth ($I = I_1 = I_2$) is analysed in detail in Chapter 2. In summary, for sufficiently low growth rate differentials x , the more fecund species 1 can competitively exclude the rapidly growing species 2, both in the presence of disturbance and in a temporally homogeneous environment. For intermediate x , coexistence is possible in the homogeneous environment, and this behaviour persists for low intensity or low frequency disturbances. As disturbance intensity increases (providing the frequency f is greater than the expected time to extinction $t_{extinct}$), the fecundity advantage of species 1 will lead to it competitively excluding species 2. Thus, disturbance can lead to a decrease in diversity. When $x > x_{max}$ is large, species 2 will exclude the more fecund species 1 due to its superior growth rate. In this case, disturbance has a more complex effect. For frequencies f such that $1/f > t_{extinct}$, intermediate disturbances will lead to coexistence of two species, while high intensities

will allow the previously excluded species 1 to claim all sites and exclude species 2. Low intensities are insufficient to change the temporally homogeneous diversity, although may extend the time to coexistence. When $1/f < t_{\text{extinct}}$, species 2 will persist in monoculture. System size impacts the region of coexistence by increasing t_{extinct} , extending the region of more complex behaviour.

For a large system, or disturbances more frequent than t_{extinct} , the range of intensities that can give coexistence varies with the growth rate differential x , and is maximised at $x = x_{\text{max}}$, and also with the difference in fecundities. As seed numbers are varied, the maximum range of disturbance is at the point $s_1 = s_2 \exp(s_2 x)$. That is, the range is maximised when the function $I = 1 - \ln(s_1/s_2)/(s_2 x)$, formed by setting $\text{AverageChange}(1) = 0$, returns $I = 0$.

3.2. Fecundity-defence trade-off. When species have identical growth rates ($x = 0$), yet differ in disturbance response and fecundities s_i , it is possible to find analytically the range of I_1-I_2 space that gives coexistence for given fecundities s_i . Setting $\text{AverageChange}(1) = 0$ and solving for I_1 gives

$$\begin{aligned} I_1 &= \frac{I_2(f(N-1)s_1 - A(1)s_2(N-1)) + A(1)(s_1 + s_2(N-1))}{I_2f(N-1)(s_1 - s_2) + fs_2(N-1) + A(1)s_1} \\ &= \frac{\alpha_1 I_2 + \beta_1}{\gamma_1 I_2 + \delta_1} \end{aligned} \quad (7)$$

while setting $\text{AverageChange}(N-1) = 0$ gives the curve

$$\begin{aligned} I_1 &= \frac{I_2(f(N-1)s_1 - A(N-1)s_2) + A(N-1)(s_1(N-1) + s_2)}{I_2f(N-1)(s_1 - s_2) + fs_2(N-1) + A(N-1)s_1(N-1)} \\ &= \frac{\alpha_{N-1} I_2 + \beta_{N-1}}{\gamma_{N-1} I_2 + \delta_{N-1}} \end{aligned} \quad (8)$$

where $A(n) = (1-f)(P(\text{increase}(n)) - P(\text{decrease}(n)))$ is constant in I_2 . The region of coexistence is therefore the area between the two curves, as demonstrated in Figure ??(a). By noting that the indefinite integral of $(ax+b)/(cx+d) = ax/c + (bc-ad) \ln(d+cx)/c^2$, we can write a solution for the size of the region of I -space that can give coexistence;

$$\begin{aligned} &\min \left(1, \int_0^1 dI_2 \frac{\alpha_1 I_2 + \beta_1}{\gamma_1 I_2 + \delta_1} \right) - \min \left(1, \int_0^1 dI_2 \frac{\alpha_{N-1} I_2 + \beta_{N-1}}{\gamma_{N-1} I_2 + \delta_{N-1}} \right) \\ &= \min \left(1, \frac{\alpha_1}{\gamma_1} + \frac{(\beta_1 \gamma_1 - \alpha_1 \delta_1)(\ln(\delta_1 + \gamma_1) - \ln(\delta_1))}{\gamma_1^2} \right) \\ &\quad - \min \left(1, \frac{\alpha_{N-1}}{\gamma_{N-1}} - \frac{(\beta_{N-1} \gamma_{N-1} - \alpha_{N-1} \delta_{N-1})(\ln(\delta_{N-1} + \gamma_{N-1}) - \ln(\delta_{N-1}))}{\gamma_{N-1}^2} \right). \end{aligned} \quad (9)$$

The minimum is taken because for sufficiently large s_1 , the function given by (??) is greater than one for all $I_2 \in (0, 1)$, but an intensity of greater than 1 is impossible. Hence, the region of coexistence does not change with s_1 in a smooth manner, as shown in Figure ??(d). The peak range of coexistence is given by intermediate s_1 (for fixed $s_2 = 50$), with the region tending to zero as the difference in species fecundities tends to infinity. For the chosen parameters, with system size $N = 1000$ the peak probability of coexistence (when intensities for the two species are chosen at random) is approximately 0.0120.

Increasing frequency also has a dramatic effect on the results. For very low frequency, no defence response combination is unable to overcome the fecundity disadvantage and allow species 2 to survive. As frequency is increased, then very high I_1 can combine with low I_2 to give a small region of coexistence. For example, if a species devoted a great

(a) (b)
(c) (d)

FIGURE 1. **Fecundity-defence trade-off:** (a) An example of the region of coexistence. The blue area (top and left) is where species 1 can invade when rare, while the pink area (bottom and right) gives the region where species 2 can invade. The region where they overlap is the region that gives coexistence with $N = 100$. (b) When system capacity is large ($N = 1000000$ here) coexistence cannot occur. (c) The change in the likelihood of coexistence as f is increased. Note that the region is maximised for low frequency disturbances. (d) The change in the likelihood of coexistence as s_1 is increased. Note the discontinuity where $(?)$ becomes greater than one. Parameters $s_1 = 500, s_2 = 50, N = 1000, f = 0.2$ unless specified.

deal of resource to surviving fire, it could persist with a species very vulnerable to fire but with a greater fecundity to spread after the disturbance. The range of parameters I_i that give coexistence in this way increases with frequency until a threshold is reached (see Figure ??(c)) at which point, it is possible for species 2 to outcompete species 1 if $I_2 < I_1$. The region of I -space then begins to decline in area and move towards the curve $I_1 = I_2 s_1 / (I_2 s_1 + s_2(1 - I_2))$. In the limit as $f \rightarrow 1$ where ‘disturbance’ events are so frequent as to provide an homogeneous environment themselves, both functions given by $(?)$ and $(?)$ reach this curve, and coexistence is not possible. If $I_1 > I_2 s_1 / (I_2 s_1 + s_2(1 - I_2))$ then species 2 will dominate the environment, while if $I_1 < I_2 s_1 / (I_2 s_1 + s_2(1 - I_2))$ species 1 will exclude the less fecund species 2.

As system capacity N increases, the range of coexistence shows a peak at low $N \approx 20$. For wood or forest sized systems, the region will decline rapidly with increased system capacity. When the system capacity tends to infinite, the region of I -space giving coexistence tends to zero. A fecundity-defence trade-off cannot sustain two species in a large system, and has little effect in assisting biodiversity when system size is that of a forest or wood.

3.3. Growth-defence trade-off. A growth-defence trade-off ($s_1 = s_2 = s$) responds to changes in system capacity and frequency in a very different manner to the fecundity-defence trade-off outlined above. Here frequency has little effect providing $1/f < t_{extinct}$, while if this condition is not satisfied, the faster growing species will exclude its competitor for any disturbance intensity regime. The response to system size is similar to that of the fecundity-growth trade-off, where as system size increases, $t_{extinct}$ will also increase towards infinity and therefore frequency will not have a significant effect on the coexistence of species, while the coexistence region of I -space will asymptote to that given by an infinitely large system. Therefore, we consider the case as $N \rightarrow \infty$ in order to simplify the calculations, while retaining the qualitative behaviour of the system. In this case, setting $\text{AverageChange}(1) = 0$ gives

$$I_1 = \frac{\exp(-x_s(1 - I_2))I_2}{1 - I_2 + \exp(-x_s(1 - I_2))I_2}, \quad (10)$$

where $x_s = sx$ is used to reduce the number of non disturbance parameters to one. Setting $\text{AverageChange}(N - 1) = 0$ gives a quadratic in I_1 , with roots given by

$$I_1 = \frac{1 + x_s(1 - I_2) \pm \sqrt{(1 + x_s(1 - I_2))^2 - 4I_2x_s(1 - I_2)}}{2x_s(1 - I_2)}. \quad (11)$$

For the wide range of x_s considered here, the root where the positive square root is taken is always above one, and therefore outside the possible parameter space for disturbance intensity, while the negative square root is the solution that helps to determine the system behaviour, along with the function given by (??).

- (a) (b)
(c) (d)

FIGURE 2. Growth-defence trade-off: How I -space changes as x_s increases. (a) When $x_s = 0$ coexistence is not possible, the species with the lower intensity will exclude the other. (b) $x_s = 2$. (c) $x_s = 26$. (d) $x_s = 500$. For $x_s > 0$ there is a region of founder control (white), a region of species 1 dominance (blue, top and left), a region of species 2 dominance (pink, bottom and right) and a region of coexistence (blue and pink overlap). This region of coexistence will increase in size until $x_s \approx 26$, and then slowly decline towards zero as the faster growing species 2 dominates. Parameters $N = 1000$, $f = 0.5$

We can numerically integrate the functions given in (??) and (??) to find the area of the region of coexistence, and we can study the behaviour of the system as x_s is varied. When $x_s = 0$ and the growth rates are identical, the species with the most resistance to disturbance (lowest I_i) will exclude its competitor. As x_s is increased, four distinct regions will occur, as in Figure ???. When both species display high resistance to disturbance (low I_i) there is a small region where neither $\text{AverageChange}(1) > 0$ or $\text{AverageChange}(N - 1) < 0$ are satisfied, and founder control occurs, where coexistence does not occur and the successful species depends on the initial populations, subject to stochastic noise. When both species have higher intensities, there exists a region where coexistence is expected. Together the two regions of coexistence and founder control form a band from across I -space that separate regions where species and species 2 will exclude the other. We find the region of coexistence peaks at intermediate $x_s \approx 26$, although the region of coexistence is very small even at this peak (approximately 0.0114). As x_s increases beyond this, the region of coexistence declines and tend to the region of I -space where $I_2 \gg I_1$, eventually tending to zero as x_s tends to infinity.

While the growth-defence trade-off can sustain two populations in a large system, the probabilities remain very small. A study of varied N suggests that the system is approximated well by the large system limit for $N > 300$, so within a large forest it is unlikely that a trade-off between growth and disturbance resistance will sustain a large number of species.

3.4. Three dimensional trade-off. When species are allowed to vary in all three traits, fecundity, growth and defence, the model responds to changes in frequency f or system capacity N in a similar way to the growth-defence and fecundity-growth trade-off models.

Frequency only affects coexistence when $1/f < t_{\text{extinct}}$, and system size removes the effect of frequency by increasing the time to extinction t_{extinct} . Therefore, as in the case of the growth-defence trade-off, the model is considered to have large system capacity (taken as the limit as $N \rightarrow \infty$). We can then solve $\text{AverageChange}(1) = 0$, which gives

$$I_1 = \frac{s_1 I_2 \exp(-s_2 x(1 - I_2))}{s_2(1 - I_2) + s_1 I_2 \exp(-s_2 x(1 - I_2))}. \quad (12)$$

Solving $\text{AverageChange}(N - 1) = 0$ once again gives a quadratic in I_1 , which has roots

$$\begin{aligned} & \frac{I_2 s_1 + s_2(1 - I_2) + s_1 s_2 x(1 - I_2)}{2 s_1 s_2 x(1 - I_2)} \\ & \pm \frac{\sqrt{(I_2(s_2 + s_1(s_2 x - 1)) - s_2(1 + s_1 x))^2 - 4 I_2(1 - I_2) s_1^2 s_2 x}}{2 s_1 s_2 x(1 - I_2)}. \end{aligned} \quad (13)$$

As in the growth-defence case, the root with the negative square root is the one that controls the behaviour of the system. Numerically integrating, we can again calculate the region of coexistence in I -space. The region of coexistence in I -space is shown in Figure ??(a). Calculating the areas of coexistence shows that for fixed seed numbers, the size of the area of coexistence will peak at intermediate values of x , while for fixed x , the range of coexistence will increase as the discrepancy in fecundities becomes more pronounced. This increase will asymptote to the point where it is not possible for species 2 to exclude species 1, but where a significant proportional of trait space will give coexistence (See Figure ??(b,d)). The region of coexistence generated by this model is consistently of an order of magnitude larger than that of the other two models (with $s_1 = 500$, $s_2 = 50$, we see that the maximum range of coexistence is given when $x \approx 0.0489$, and this region of coexistence has area ≈ 0.164)

(a) (b)
(c) (d)

FIGURE 3. **Three-dimensional trade-off:** (a) An example of I -space. The pink region to the bottom and right are where species 2 is dominant, while the blue region (top and left) give species 1 monoculture. Where these regions overlap there is coexistence. (b) When s_1 tends to infinity, there is still a significant region of space that gives coexistence, although species 2 dominance is almost impossible ($s_1 = 5 \times 10^{10}$). (c) The change in the region of coexistence as x varies, with a peak at intermediate values. (d) The size of the region given in (b) asymptotes as s_1 increases. Parameters $s_1 = 500$, $s_2 = 50$, $x = 0.06$, $N = 1000$, $f = 0.5$ used to generate images unless specified.

3.5. Linked intensities. However, it is perhaps unrealistic to allow the responses to disturbance to move at random through I -space. Species specific responses are likely to be linked, such that as one increases, the other also increases. To simulate this, we consider the case where $I_1 = y I_2$, such that y is a measure of the differences in the life history strategies of the two species, and I_2 is the force of a given disturbance event, normalised to the response of species 2. Note that for $y \neq 1$ one species will experience certain mortality

while the other may retain some individuals. As intensity increases beyond this point, the two intensities will converge at one, but as the species with the lower resistance is already doomed, this will not affect the likelihood of species coexisting.

In the three dimensional trade-off model, we consider the effects of changing y on the range of disturbances that can give coexistence for the parameters $s_1 = 500$, $s_2 = 50$, $x = 0.06$.

We can then plot the average change at the boundary as a function of I_2 for differing y . We find dramatically different behaviour as y varies. For y sufficiently large ($y > 1.39$ for the current parameters), such that species 2 has a huge advantage in survival of a disturbance event, we find that for all intensities, coexistence does not occur, and species 2 exists in monoculture. Here, the increased fecundity of species 1 is not sufficient to overcome the dual advantage of species 2, with its superior juvenile growth rate and increased resistance to disturbance, as shown in Figure ???. As y decreases, the behaviour then changes, as

FIGURE 4. Plots of $\text{AverageChange}(1)$ in blue and $\text{AverageChange}(N-1)$ in pink. $\text{AverageChange}(N-1) < 1$ is satisfied for all intensities, but $\text{AverageChange}(1) > 0$ never holds, so species 2 will exist in monoculture. $\text{AverageChange}(1) > \text{AverageChange}(N-1)$ for all I_2 .

the curve for $\text{AverageChange}(1) > 0$ is satisfied for a range of intermediate disturbance intensities. At the same time, $\text{AverageChange}(N-1)$ remains below zero for all intensities I_2 , meaning that coexistence is possible for intermediate intensities, but either side of this range species 2 will competitively exclude species 1. For the given parameters, the range of y exhibiting this behaviour is approximately $1.16 \leq y \leq 1.38$. Decreasing y further, making the two species response to disturbance more similar, we get yet more behaviour. For $y \leq 1.15$, $\text{AverageChange}(N-1)$ has two real roots, and is positive between these roots. While $y > 1$, both these roots occur in the interval $[0, 1)$, as do two roots of $\text{AverageChange}(1)$. In this case, there are four distinct responses to disturbance as it increases in intensity (see Figure ??). At low intensity, disturbance events are not strong enough to promote the more fecund species 1, so species 2 exists in monoculture. As intensity increases, then $\text{AverageChange}(1) > 0$ is satisfied, while $\text{AverageChange}(N-1) < 0$ continues to hold, giving coexistence of both species. Further increasing intensity, however, will result in $\text{AverageChange}(N-1)$ becoming positive. Here, species 2 will be competitively excluded, and species 1 will monopolise the system. Increasing intensity yet further results in $\text{AverageChange}(N-1)$ dropping back below zero, to give a secondary region where our invasion analysis predicts coexistence. However, for the parameters studied here, the intensity here is high, and leaves a small remaining population (when $N = 1000$, the remaining population is, on average, approximately 30 individuals). This reduced population is very susceptible to the stochasticity in the model, and all simulations result in one species going extinct by chance, although the identity of the surviving species varies between simulations. Increasing intensity even more, we have that $\text{AverageChange}(1)$ also drops below zero, so the theory predicts species two monoculture, which is once again matched by simulations, even given the extremely high intensities involved.

Once $y \leq 1$ there is only one root of $\text{AverageChange}(1)$ and one root of $\text{AverageChange}(N-1)$ in the interval $(0, 1)$ (See Figure ??). We therefore see a different type of behaviour again, with species 2 excluding the more fecund species 1 at low intensities, coexistence occurring at intermediate intensities, and species 1 excluding species 2 as high intensities.

FIGURE 5. Plots of $\text{AverageChange}(1)$ in blue and $\text{AverageChange}(N - 1)$ in pink. Both curves have two real roots in the interval $[0, 1]$, resulting in two bands of coexistence predicted by theory, with alternating monocultures surrounding them, species 2 monoculture at low and very high intensities, and species 1 at intermediate intensities. Note the higher band of predicted coexistence is not conformed by simulations, instead experiencing extinction of a random species due to the high intensity of disturbance events. $\text{AverageChange}(1) > \text{AverageChange}(N - 1)$ for all I_2 .

FIGURE 6. Plots of $\text{AverageChange}(1)$ in blue and $\text{AverageChange}(N - 1)$ in pink. Both curves have a single real root in the interval $[0, 1]$, resulting in a band of coexistence predicted by theory at intermediate intensity, with species 2 dominating at lower intensities while species 1 dominates at high intensities. $\text{AverageChange}(1) > \text{AverageChange}(N - 1)$ for all I_2 .

As y decreases towards zero, the range of intensities that can support both species will tend to a small interval, of with approximately 0.005, at very low intensities ($0.005 \lesssim y \lesssim 0.01$). We find that it is possible only to slightly increase the range of intensities giving coexistence from that of the case $y = 1$, with $y = 0.90$ (2 significant figures) giving a small increase in intensity range leading to coexistence ($0.4666 > 0.4663$), but this value declining again for y below this point. That is, when the more fecund species 1 has a slight advantage in resistance to disturbance, the range of disturbances that the system can survive while maintaining it's full biodiversity is maximised.

4. DISCUSSION

Both life history trade-offs and disturbance events have been suggested as mechanisms that can promote and support high levels of diversity in nature. Here, we demonstrate that trade-offs among the three major life history traits for plants can give coexistence of at least two species competing within the same niche, and numerically quantify the likelihood of coexistence for each trade-off. However, the effectiveness of these trade-offs in supporting multiple species varies dramatically. Where species do not differ in juvenile growth rates, only small communities can possibly support more than a single species, and even in these small communities coexistence is extremely unlikely. This result suggests that a trade-off between seed production and resilience cannot realistically contribute to the diversity of a community, a view supported by the lack of empirical evidence in favour of this trade-off. **Using data from [?], [?] concluded that “it is unlikely that... survivorship come[s] at the expense of fecundity.” While some other studies find a correlation between (e.g. [?, ?]) this relationship is often weak, suggesting that the selection pressure for such a trade-off is weak. We propose that evidence for this trade-off is a consequence of other, more strongly selected trade-offs such as the growth-survival and fecundity-growth trade-offs.**

Meanwhile, trade-offs between growth and either fecundity or disturbance (or both) resistance can support multiple species for any system capacity N . This result c In a large system, we demonstrate that a trade-off involving all three of the major plant traits will

give a probability of randomly selected disturbance resistances supporting two species an order of magnitude higher than the probability given by a growth-defence trade-off alone. However, when species responses to disturbance are proportional (such that disturbance intensity for one species is doubled, the intensity for the second species is also doubled), the three dimensional trade-off does not significantly improve the likelihood of coexistence when compared to a fecundity-growth trade-off. These results suggest that the trade-off between fecundity and juvenile growth rate, contributes much more to the maintaining of high biodiversity than trade-offs involving disturbance resistance.

While varying frequency of disturbance can have very different effects when compared with altering the intensity of the events, we find that trade-offs where species differ in growth rate display a almost constant relationship with any frequency such that the expected time between disturbances. **Because the probability of a species 1 death scales linearly as the population of species 1 increases, the exponential increase in the probability of colonising a gap when species growth rates differ allows the overlap of the two invasion criteria. However, in the case where species only differ in fecundity and defense, both the likelihood of death and colonisation of a given species change linearly, resulting in a more complex relationship with frequency, as the differences in the colonisation and death probabilities do not change in a sufficiently different manner to override the effect of changing frequency.** When species differ in fecundity and defence allocation, but not growth, frequency effects differ, although these effects are of limited interest as this trade-off struggles to support multiple species under any disturbance regime.

We conclude that a trade-off between fecundity, in the form of per capita annual seed production, and juvenile growth rates is much more significant in sustaining biodiversity than trade-offs between growth and defence or fecundity and defence, and while species specific reactions to disturbance can slightly improve the likelihood of a fecundity-growth trade-off allowing two species coexistence, this increase is not significant. This concurs with empirical studies, which have found a great deal of support for a trade-off between fecundity and growth rate, or the equivalent competition-colonisation trade-off (e.g. [?, ?, ?, ?]). The high level of occurrence for this trade-off indicates that it has been an important driver in the evolution of those diverse communities, allowing two or more species to effectively occupy the same resource niche by the different allocation of that resource to their life history traits. That a trade-off between growth and defence can support some coexistence suggests that some support should be found for this trade-off in empirical studies, and this is indeed the case (e.g. [?, ?]). However, support for this is much less widespread than the fecundity-growth or competition-colonisation trade-off, which further supports our conclusion that the latter is the most significant driver of biodiversity.