

Towards a mechanistic understanding of dispersal evolution in plants: conservation implications

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ABSTRACT

Aim A species' dispersal characteristics will play a key role in determining its likely fate during a period of environmental change. However, these characteristics are not constant within a species – instead, there is often both considerable interpopulation and interindividual variability. Also changes in selection pressures can result in the evolution of dispersal characteristics, with knock-on consequences for a species' population dynamics. Our aim here is to make our theoretical understanding of dispersal evolution more conservation-relevant by moving beyond the rather abstract, phenomenological models that have dominated the literature towards a more mechanism-based approach.

Methods We introduce a continuous-space, individual-based model for wind-dispersed plants where release height is determined by an individual's 'genotype'. A mechanistic wind dispersal model is used to simulate seed dispersal. Selection acts on variation in release height that is generated through mutation.

Results We confirm that, when habitat is fragmented, both evolutionary rescue and evolutionary suicide remain possible outcomes when a mechanistic dispersal model is used. We also demonstrate the potential for what we term evolutionary entrapment. A population that under some conditions can evolve to be sufficiently dispersive that it expands rapidly across a fragmented landscape can, under different conditions, become trapped by a combination of limited dispersal and a large gap between patches.

Conclusions While developing evolutionary models to be used as conservation tools is undoubtedly a challenge, we believe that, with a concerted collaborative effort linking the knowledge and methods of ecologists, evolutionary biologists and geneticists, it is an achievable aim.

Keywords

Biological invasions, climate change, dispersal, evolution, exotic species, range shifting.

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INTRODUCTION

Dispersal is a key life history characteristic for both ecology and conservation biology, playing a major role in determining how well populations respond to habitat fragmentation (e.g. Thomas, 2000; Trakhtenbrot *et al.*, 2005) and determining how able they are to shift their biogeographic range as climate changes (e.g. Higgins & Richardson, 1999; Pearson & Dawson, 2005). Additionally, an invasive species' dispersal characteristics determine how rapidly it spreads into non-native habitat (e.g. Harris *et al.*, 2009; Trakhtenbrot *et al.*, 2005). Increasingly, we are interested in making predictions regarding the

future population size or future biogeographic range of species and to make these predictions we typically make use of spatial models. Although dispersal ecologists have made considerable progress developing sophisticated mechanistic models of the dispersal process, these are yet to be widely used within applied fields. Similarly, while there is now considerable theoretical and empirical support for the idea that dispersal traits are highly labile, and that their evolution may influence spatial dynamics, this has yet to be translated into more applied areas of conservation biology. Our aim in this contribution is twofold: first, to demonstrate how existing and generally quite abstract theory relating to dispersal evolution can be linked

with mechanistic models of seed dispersal by wind and, second, to argue that by acquiring a more mechanistically based understanding of how dispersal-related traits evolve we will be better placed to test theory and, thus, to provide conservation-relevant recommendations.

A large existing literature is concerned with the evolution of dispersal (see Bowler & Benton, 2005 and Ronce, 2007 for reviews) and here we will summarise the key findings before highlighting how we believe the existing theory should be extended. Several strong selective forces act to favour movement of individuals between patches. As temporal environmental variability (McPeck & Holt, 1992; Travis, 2001) and/or demographic stochasticity (Travis & Dytham, 1998; Cadet *et al.*, 2003) increase, selection favours greater rates of dispersal (Olivieri *et al.*, 1995; Metz & Gyllenberg, 2001). This selection pressure comes about as a consequence of the increased rate at which local populations suffer extinctions as temporal environmental and demographic stochasticity increase; under these conditions individuals that colonise an empty patch receive substantial intergeneration fitness benefits. Selection also favours dispersal as it reduces both kin competition (Gandon, 1999; Ronce *et al.*, 2000; Bach *et al.*, 2006) and inbreeding (Gandon, 1999; Motro, 1991; Perrin & Mazalov, 2000). While these factors all exert upwards selective pressure on dispersal, its evolution is constrained by several potential costs. There may be considerable energetic costs associated with effective dispersal between patches (Zera & Mole, 1994) – in plants these energetic costs are likely to relate to the energetic costs of producing flight apparatus (such as wings), seed propulsion mechanisms or, for animal-mediated dispersal, structures that result in adhesion of seeds to fur. In addition to these physiological costs, a dispersing seed may finish its journey at an unsuitable location.

The majority of modelling related to dispersal evolution is extremely abstract and general in nature and is not readily extendable to particular species or landscapes (but see Heino & Hanski, 2001; Phillips *et al.*, 2008). In the most part, this theory has sought to identify the evolutionarily stable rate, or probability, of emigration from a natal habitat patch (e.g. McPeck & Holt, 1992; Travis & Dytham, 1999). Typically, this is a condition independent rate although, in recent years, we have gained some initial insight into how condition-dependent dispersal evolves (e.g. Travis *et al.*, 1999). Clearly, for most applied ecological questions, it is not simply a density-independent or density-dependent rate of emigration that will determine the population-level outcome (e.g. probability of persistence, rate of range expansion). In most cases, the probability distribution of dispersing different distances (the dispersal kernel) is key. However, only a few studies have developed theory exploring the evolution of dispersal kernels (Hovestadt *et al.*, 2001; Murrell *et al.*, 2002; Rousset & Gandon, 2002) and while these studies have used different model formulations, they all have one thing in common; the modelling of dispersal is in no way mechanistic.

While most spatial models incorporating distributions of dispersal distances have done so phenomenologically, progress

in mechanistic modelling of dispersal is starting to result in a shift in emphasis. There are now a suite of models available that model the dispersal distances of wind-dispersed seeds by explicitly accounting for wind characteristics and key plant traits such as seed terminal velocity and the release height of seeds (Nathan *et al.*, 2001; Tackenberg, 2003; Katul *et al.*, 2005), and these models have already been used within studies predicting the rate of range expansion of plant species (e.g. Harris *et al.*, 2009). However, to date these methods have not been used within an evolutionary context.

In this contribution, we make an initial step towards being able to better link theoretical models of dispersal evolution with empirical work on dispersal ecology by introducing a model where seed release height is allowed to evolve. Subsequently, we use the model to demonstrate that the rapidly emerging field of conservation biogeography (Richardson & Whittaker, 2010) can benefit from an evolutionary perspective. Key challenges for conservation biogeography include describing, understanding and managing changes in the spatial distributions of invasive species (e.g. Leung *et al.*, 2010; Thuiller *et al.*, 2010), and studying the response of species' distributions to climate change (e.g. Mustin *et al.*, 2009; Ackerly *et al.*, 2010; Thomas, 2010): we emphasise that dispersal (through selection on seed release height) can have important implications in both of these key areas.

THE MODEL

The model that we develop has certain characteristics that are common to numerous previous studies of dispersal evolution but, in other respects, it is distinctly different. As in most previous models, we assume the population has discrete, non-overlapping generations and we assume haploid individuals that inherit their phenotype from their parent with a small probability of mutation. However, whereas in previous models the heritable trait has been the propensity to emigrate (McPeck & Holt, 1992; Travis & Dytham, 1999; Travis *et al.*, 2009) or the mean dispersal distance (Murrell *et al.*, 2002; Gros *et al.*, 2006; Dytham, 2009), here we take a rather more mechanistic approach and allow height of seed release to evolve. Evolution of this trait comes at a cost; we assume a trade-off between investment in growth resulting in increased release height and investment in seed production. Below we describe, in turn, how we represent the environment, our individual-based model of ecological and evolutionary dynamics and finally, the simulation experiments that we conduct.

The environment

We employ a continuous space representation of the landscape where patches of suitable habitat are embedded in a hostile matrix within which individuals never survive or reproduce. For simplicity, we assume circular patches of suitable habitat which are of equal size and quality. The patches are randomly distributed with the only constraint being that they are not allowed to overlap. An example of the landscape structure can

be seen in Fig. 1. We assume that patches all have the same diameter. In some simulations, we also incorporate patch extinction. At each generation, there is a probability, P , that all individuals in a patch die. These local extinction events can be thought of as arising because of local weather events or anthropogenic disturbances.

The ecology

In each time step, an individual plant produces a number of seeds taken from a Poisson distribution with mean S . In previous models of dispersal evolution these seeds would, depending upon the model, have been dispersed either (1) to any patch on the landscape with equal likelihood, (2) to any one of the neighbouring patches with equal likelihood or (3) a distance drawn from a constant statistical distribution – most often, the negative exponential. Here, we instead simulate the dispersal of seeds using a mechanistic dispersal model. There are several such models available with varying complexity (e.g. Nathan *et al.*, 2001; Tackenberg, 2003; Katul *et al.*, 2005). For illustration, we have chosen to use one of the simplest possible models, WINDISPER (Nathan *et al.*, 2001; Stephenson *et al.*, 2007), but the general approach for incorporating evolution of traits would be very similar if other dispersal models were selected. For full details of the physical derivation of this particular mechanistic dispersal model see Nathan *et al.* (2001). Using this model, the distance that a seed is dispersed is drawn from a negative exponential distribution that depends

upon the seed's terminal velocity, the height from which it is released, the horizontal (and potentially vertical) wind speed and two roughness parameters, d and z_0 , which relate to the height of vegetation over which the seed will be dispersed (see Nathan *et al.*, 2001). In all the simulations presented here, we used $d = 0.066$ and $z_0 = 0.03$, corresponding to a vegetation height of approximately 5–15 cm (Stephenson *et al.*, 2007).

Each seed has its terminal velocity sampled from a normal distribution, and in all our simulation experiments we sampled from a distribution with mean = 0.98 and standard deviation = 0.14. The wind speed on which each seed is released is sampled from the normal distribution with mean = 2.2 ms^{-1} and standard deviation = 0.58 ms^{-1} . These are arbitrary values but are taken from some of our wind speed measurements over a period of a week taken on the west coast of Scotland. We assume that the release height is identical for all seeds released from one individual plant, although it would be straightforward to relax this assumption in future work. It is important to note that while the expected distribution of distances for any one seed will be negative exponential, each seed has its terminal velocity independently drawn from a distribution and is dispersed on a wind speed drawn from another distribution. Thus, the shape of a plant's (or a population's) dispersal kernel will be a function of these two distributions as well as the negative exponential from of WINDISPER.

Once all seeds have been dispersed, we simulate juvenile competition. We assume that all seeds germinate and that the

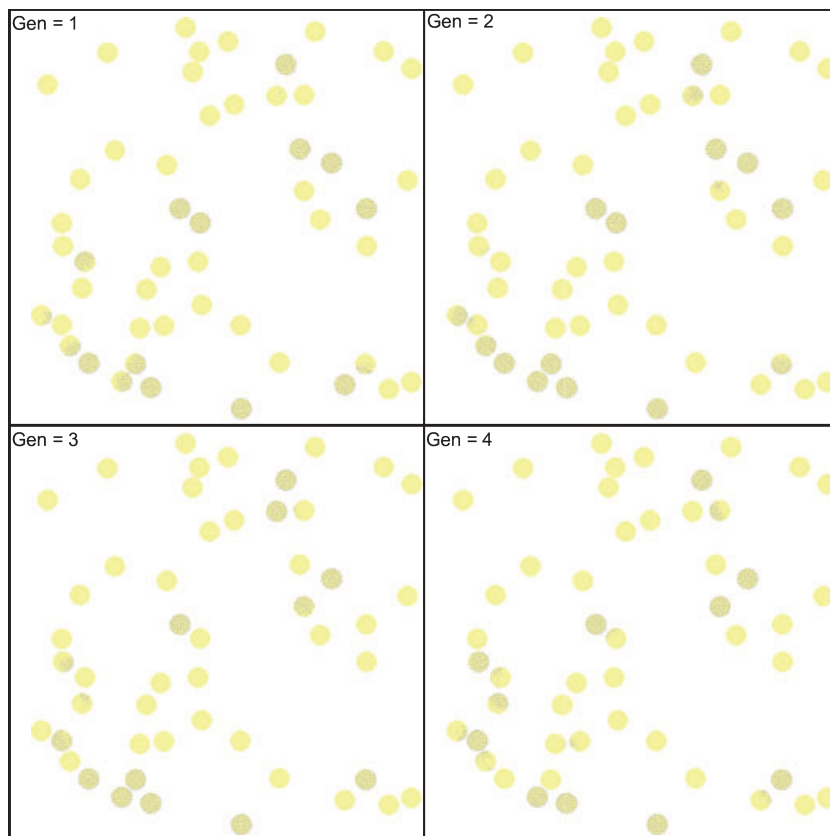


Figure 1 A typical model landscape and an example of spatial population dynamics over four successive generations. The yellow circles represent suitable habitat patches within an inhospitable matrix. The black dots show plants. In this example there is regular local extinction of populations ($P = 0.4$). The recolonisation dynamics can be clearly seen.

survival of each juvenile plant is dependent on the density of plants within its local neighbourhood. The neighbourhood of an individual located at (x,y) is defined as the circle of radius n around (x,y) , where n specifies the neighbourhood size. Based on the method of Pacala & Silander (1985) and to save computer time, neighbours of an individual located at (x,y) are calculated without the need to check distances between a focal plant and every other individual on the landscape. First, a grid with square cells of size n is placed over the landscape, and at each generation, all plants within each cell are recorded. If the point (x,y) is located at the corner of a grid cell, the nearest four cells will be searched for neighbours. Otherwise, the nearest six or nine cells are searched. The interaction strength between a focal individual and each of its neighbours is calculated as

$$i = 2.0 - v/n,$$

where v is the distance between the individual and its neighbour. This method implies that a neighbour at the same location has twice the influence as a neighbour a distance n away and is taken from Travis (2003). Density is then calculated as the sum of the interaction strengths between an individual and all its neighbours, divided by the area of the neighbourhood (to eliminate edge effects). Juveniles fail to survive when the density they experience is above a threshold, which we set arbitrarily to 0.05 in all the experiments described in this experiment.

It is assumed that the plant is an annual species, and thus after reproducing, all individuals die.

Incorporating evolution

Each plant carries a single gene that determines the height of seed release. At initialisation, all individuals carry the same gene and in subsequent generations individuals inherit this gene from their parents with a probability m of mutation. In all the results shown in this paper, $m = 0.05$, although we do run some simulations with $m = 0.1$ and $m = 0.001$ to check that results are qualitatively similar. Given our assumption of a trade-off between a greater height of seed release and seed production, this gene also determines the expected seed production of a plant. We assume the following relationship for this trade-off:

$$S = S_0 - c * Ht$$

where S_0 is the mean seed production when the release height, $Ht = 0$ and c is the cost to seed production of having a 1 m taller inflorescence. In all runs of the model for which results are shown, $S_0 = 40$. We have also conducted some runs of the model where S_0 has been varied between 30 and 120.

SIMULATION EXPERIMENTS

Before conducting our experiments, we generate some data to demonstrate how the dispersal kernel depends upon release

height. We simulate the dispersal of 10,000 seeds from plants that have, in turn, release heights of 0.5, 1.0, 1.5 and 2.0 m.

Experiment 1

We run sets of simulations to establish how long it takes for any steady state to be reached. For a range of parameter values, we run the model multiple times for different starting values of release height. We monitor the evolutionary and population dynamics over time. This is an important step in any evolutionary modelling of this type. It is required to determine how long to run simulations for before we collect 'equilibrium' data or before we perturb the system with, for example, habitat loss or range expansion.

Experiment 2

We explore how release height evolves in a scenario where the amount of suitable habitat is reduced. Initially we allow a population to establish on a landscape with 60 patches. All the initial plants have a release height of 0.5 m. After 1000 generations, we remove 45 patches at random and track the subsequent population and evolutionary dynamics. Our example scenario is for a landscape 400 m by 400 m in size and where all patches have diameter = 15 m. These patches suffer local extinction with probability $P = 0.1$.

Experiment 3A

In this experiment, we consider the evolution of release height during range expansion. Here, we modify the shape of the landscape so that it is much longer (12,000 m) than it is wide (100 m). Patches are all 20 m diameter. We allow a population to establish at the left hand side of the landscape (the leftmost 300 m) and restrict it to this region for sufficiently long that it obtains equilibrium. Then we allow the population to spread across the landscape and, through time, we monitor both the height of release in the population and the rate of range expansion.

Experiment 3B

This experiment was designed to explore in greater detail an effect we observed in the results of Experiment 3A. Again we simulate range expanding populations but, to generate some more readily interpretable results, we simplify the landscape by making it one dimensional. The landscape is now represented as a string of patches. By reducing the complexity of the landscape, the time taken to run individual simulations is substantially reduced and we are therefore able to run more repetitions of the model; in this experiment, we run 100 repetitions for each combination of parameters. As in 3A, the patches are all 20 m diameter. In all but one case, the distance between the centres of adjacent patches is the same and in all the results shown here it is 30 m. Just one of the gaps between adjacent patches is set to be larger, and its size is specified by a

parameter, g . In addition to varying the size of the unusually large gap, we vary its location: p specifies the number of patches from the left that it occurs. Thus, if p is a low number the larger gap occurs close to where the range expansion commences and when p is larger, range expansion proceeds for longer before the unusual gap is encountered. Figure 2 provides a schematic of the model used in this experiment.

RESULTS

The distribution of dispersal distances (dispersal kernels) travelled by seeds from a single plant depends upon the release height (Fig. 3). As expected, as the height of release increases the mean distance travelled by a seed increases. We have plotted the dispersal kernels in the standard way as histograms, but have also shown the positions that seeds have travelled to in 2D to aid interpretation of the results we gain when release height evolves on patchy landscapes.

Experiment 1

In general, the height of release has evolved to a steady state after a few hundred generations although sometimes the transient phase can last longer (results not shown in a separate figure but reasonable evolutionary stability is evident in Figs 4 & 6 in the periods prior to habitat loss and range shift, respectively).

As is often the case in stochastic models of this type, there can be considerable fluctuation around the equilibrium over time. We obtain qualitatively similar results with both higher

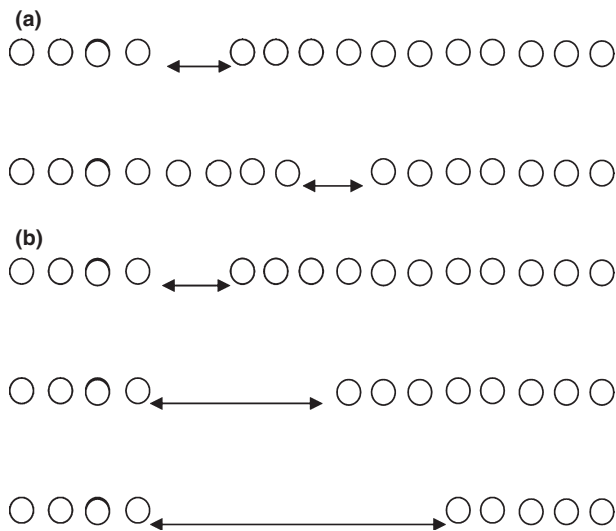


Figure 2 Schematic showing the design of Experiment 3B. In this experiment we represent the landscape as a string of patches. The distance between adjacent patches is constant except for one gap which is unusually large. (a) represents scenarios where the position of the unusually large gap is varied while (b) shows gaps of different size that are in the same position. We run simulations varying the position and the size of the gap and determine how the time taken to cross the gap depends upon these parameters.

and lower mutation rates. The equilibrium is obtained more rapidly when higher mutation rates are used, but there is also greater fluctuation about a mean. In simulations across which we vary the potential for seed production by adjusting S_0 , we find that greater release heights evolve when seed production is increased (i.e. S_0 is higher). Interestingly, some of our observations of the model are suggestive of alternative or multiple attractors. Because of this, in some regions of parameter space, the starting conditions may become very important; if populations are initialised with relatively short plants then the plants may tend to stay short, while if they start tall they may tend to stay tall. It is outside the scope of this study to investigate this potential effect in detail, but it is important for future work that this possibility is highlighted here.

Experiment 2

Our results for this habitat loss scenario can be characterised as falling into two main categories. Of the 10 simulations, we had four examples where the population became extinct and six where it survived and the evolutionary and population dynamics that lead to extinction or survival can be quite different (Fig. 4 shows four examples). Following habitat loss at time = 1000, 15 patches are left on the landscape. However, the height of release that has evolved on the 60 patch landscape leads to insufficient longer-distance dispersal to maintain high patch occupancy. So, in the period immediately after habitat loss we typically observe a period when far fewer than 15 patches are occupied. This is the case in all four examples shown in Fig. 4. It is important to note that these 10 simulations were all run using the same parameter values and the variability between simulations was therefore because of either idiosyncratic features of the landscapes or stochasticity in the population dynamics or probably both.

After the initial habitat loss and reduction in patch occupancy, one of two things can happen. Either, height of release evolves upwards, leading to increased frequency of long distance dispersal and hence greater patch connectivity and occupancy (Fig. 4c,d), or it evolves downwards and the population eventually becomes extinct (Fig. 4a). Figure 4b provides a slightly more complex example where there is an initial increase in release height and some recovery of the population but, before it reaches sustainably high levels of patch occupancy, lower release heights evolve and the population ultimately goes extinct. We also note the pattern in Fig. 4d; here, there appear to be cyclic-like dynamics whereby there are periods with taller plants and high patch occupancy followed by evolution towards shorter plants resulting in lower patch occupancy and then back again to taller plants and higher patch occupancy.

There are clear relationships between the evolved height of release and both number of patches occupied and the total population size. In Fig. 5, we summarise this by plotting all data from the ten replicate simulations from each time point subsequent to habitat loss (time = 1000). In our example,

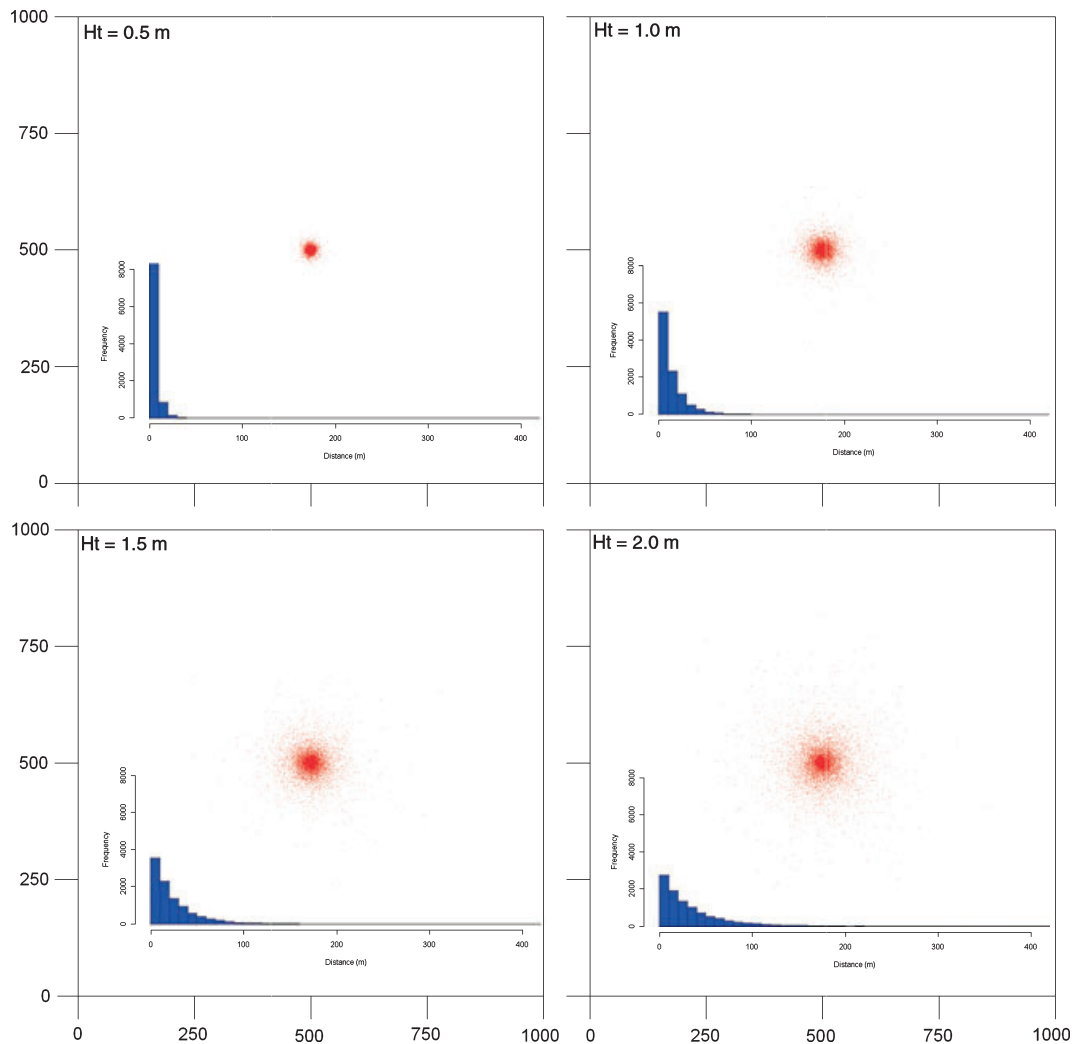


Figure 3 The height of release influences the distribution of dispersal distances travelled by seeds. Here, for four release heights, we show both the locations seeds dispersed to and, in the inset histograms, the dispersal kernels. In each case we released 10,000 seeds.

there is a straightforward pattern where increased height of release results in greater patch occupancy (Fig. 5a). However, the pattern is not as straightforward when total population size is considered (Fig. 5b). In this case, as height of release increases from 0.5 to around 0.9, there is a clear trend towards greater total population size. However, as height of release increases beyond this point, total population size levels off and then, for increases in height of release above approximately 1.2 m, there is a resulting decrease in total population size.

Experiment 3A

When we simulate a range expansion, we typically observe a substantial increase in release height and this drives an accelerating rate of spread (Fig. 6). Here we present four examples of 10 simulations that were run and we highlight some points of interest. In many runs of the model, we see a rapid and steep increase in height of release and spread rate (Fig. 6a,b typify this) although there is variability in the initial

spread rate. For example, in Fig. 6a the population immediately spreads at 20 m yr^{-1} and accelerates to spread at around 36 m yr^{-1} , while in Fig. 6b the initial spread is under 1 m yr^{-1} but it ultimately obtains a very similar spread rate to that obtained in Fig. 6a. We observe very similar equilibrium spread rates in all ten of our runs of the model. When we look at the data collected across the ten replicate runs of the model, we observe a very clear relationship between release height and rate of expansion (results not shown).

In three of the ten runs of the model, we observe an interesting effect where in the initial phase of range expansion the population becomes trapped and does not spread (Fig. 6c,d provide two examples). This occurs when there is an unusually large gap between habitat patches that the population needs to cross to continue its expansion. Once a population has crossed the gap, then selection rapidly acts to increase height and the range expansion accelerates (as in the other examples). Experiment 3B was designed to explore this effect in greater detail.

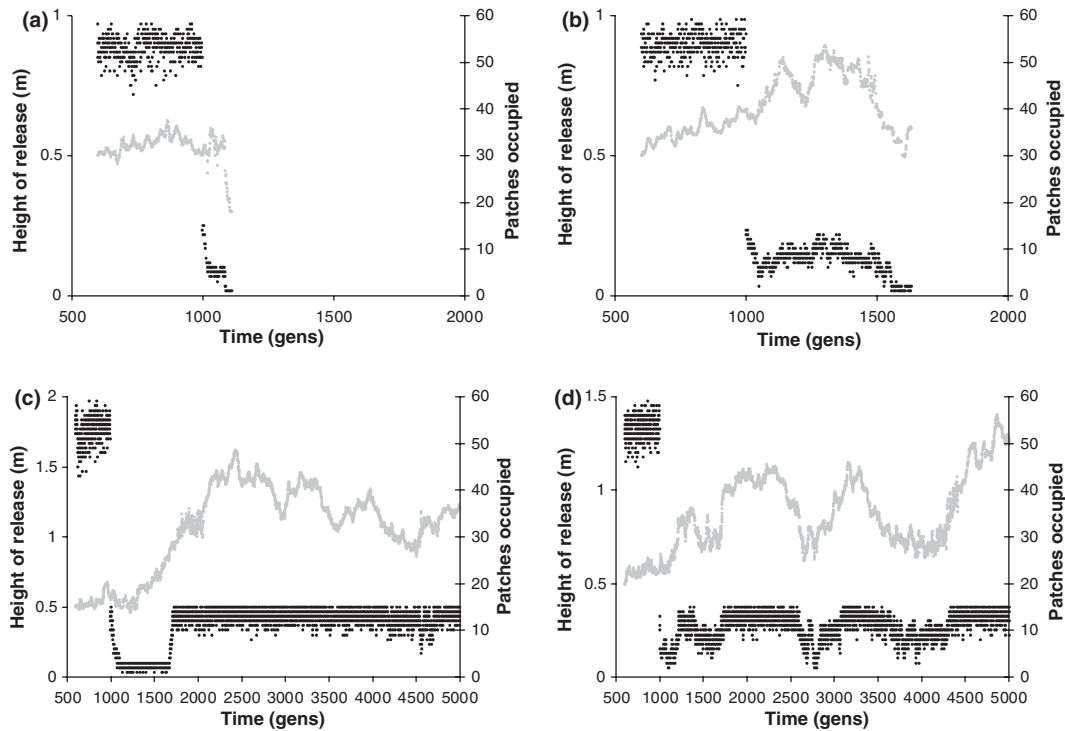


Figure 4 Both evolutionary suicide (a, b) and evolutionary rescue (c, d) can occur following habitat fragmentation. The four examples are all generated for a scenario where initially 60 habitat patches are available but at time = 1000, 45 of them are destroyed. Grey depicts the height of release and black the patch occupancy. Typically we see two types of response. First, the height of release evolves downwards making the population more vulnerable to extinction (a). Second, the height of release evolves upwards, increasing patch occupancy and securing long term population persistence (c). In some instance the dynamics are somewhat more complex. In (b) an example is shown where there is a moderate initial increase in release height, but at around time = 1300 this trend is reversed and evolution towards lower release height ultimately drives the population extinct. In (d) evolution of increased height results in population persistence but there is a suggestion of cyclic dynamics with periods where taller plants dominate followed by periods with shorter plants. In the periods when plants are shorter the patch occupancy is lower. For this figure, we selected four illustrative examples from ten runs of the model each using the same parameter values ($P = 0.1$, $c = 20.0$).

Experiment 3B

Experiments 2 and 3A present a relatively small number of independent model realisations that show some interesting dynamics for habitat loss and range expansion, respectively. Because this continuous space, evolutionary model is slow to run for a 2D array of patches, it is challenging to explore parameter space as fully as we would wish. To explore the evolutionary entrapment hinted at by some of the results from Experiment 3A, we designed an experiment using a much simpler landscape with far fewer patches. This enabled much greater repetition and fuller exploration of parameter space. Our results from this experiment show very clearly that it is possible for a range expanding population to become trapped for long periods of time, sometimes indefinitely, by a large gap in the habitat network (Fig. 7). What is most interesting is that, as long as the population has a reasonable period of range expansion before encountering a gap, it is generally able to cross the gap relatively rapidly. This is because plant height (and hence mean seed dispersal distance) has evolved upwards. It is in the early stages of a range expansion that entrapment is most likely. Unsurprisingly, the larger the gap the more likely it

is that the population is trapped, or at least has its range expansion held up for longer (Fig. 7).

DISCUSSION

Here, we have introduced a model framework where the realised dispersal kernel of a plant evolves through selection acting on the height of seed release. While our model remains quite simple, it extends almost all previous work on dispersal evolution in two important directions. First, it moves beyond previous models considering the evolution of dispersal kernels that have either allowed the parameter(s) of a statistical distribution to evolve (Ezoe, 1998; Murrell *et al.*, 2002), or have allowed the shape to evolve freely without including biological or physical constraints (Hovestadt *et al.*, 2001; Rousset & Gandon, 2002). Our approach to modelling dispersal is far more mechanistic in nature than these previous phenomenological treatments. Second, our model is able to account for likely trade-offs. In the illustrative example explored in this paper, we allow height of release to evolve, but increasing height comes at a cost. In our example, plants that invest in growing a taller inflorescence produce

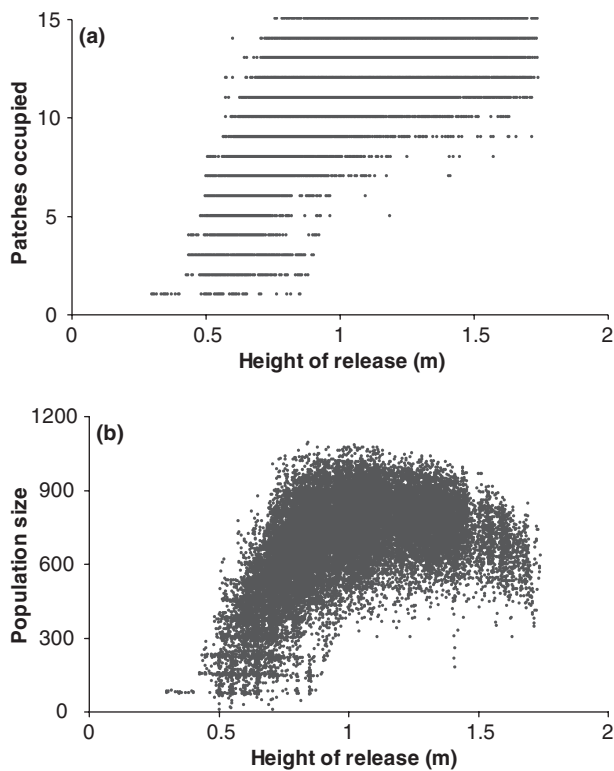


Figure 5 The relationships between height of release and patch occupancy (a) and height of release and total population size (b). The data are from time > 1020 from the same 10 runs of the model described in Fig. 4. Clearly, as height of release increases there is a trend towards greater patch occupancy (a). As height of release increases up until around 1.0 m there is a similar increase in population size. However, as height of release increases further population size levels off and even decreases.

less seeds. We believe that for models incorporating life-history evolution to have a greater impact on conservation biology they need to begin to incorporate greater biological realism. The illustrative results that we present in this paper are qualitatively consistent with those previously obtained from more abstract models. However, we consider that the model presented here is a first step towards developing more tactical evolutionary models that can directly inform conservation decision making for particular species on particular landscapes. After discussing our results, we will suggest how future work can take us closer to management models that incorporate evolution.

For wind-dispersed plants, release height is one of the most important plant attributes in determining the dispersal kernel (Soons *et al.*, 2004; Gomez, 2007). Our results (Fig. 2) highlight that mean (and maximum) dispersal distances can both increase quite dramatically as release height increases. The reason for this result is straightforward; seeds released from a greater height have a longer falling time during which they can travel a greater horizontal distance (Soons *et al.*, 2004). Additionally, the horizontal wind speed is not constant with height from the ground – thus seeds released from higher also

have a period of their fall when they are exposed to higher horizontal speeds (Nathan *et al.*, 2001). The theoretical prediction that seeds should disperse further when they are released from greater height has been confirmed in several empirical studies across a broad range of plant species (e.g. Sheldon & Burrows, 1973; Venable & Levin, 1985; Thiede & Augspurger, 1996; Wender *et al.*, 2005; Gomez, 2007).

It is important to highlight that in patchy landscapes there is often a tension between two different selective forces acting on dispersal, one tending to drive it down, the other drive it up. Previous theory (Comins *et al.*, 1980; Olivieri *et al.*, 1995; Gros *et al.*, 2006) and empirical observations (Cody & Overton, 1996; Cheptou *et al.*, 2008; Fresnillo & Ehlers, 2008; Riba *et al.*, 2009) have shown that in isolated patches, dispersal ability is typically reduced and that it is reduced more when patch areas are smaller. As the patch area reduces, the probability of seeds being dispersed outside of the patch and into unsuitable habitat increases. This effectively imposes an increased distance-dependent cost and is the mechanism driving selection in some previous work (Hovestadt *et al.*, 2001). As Riba *et al.* (2009) recently highlighted, Darwin was the first to suggest that habitat isolation should select for decreased dispersal ability. Darwin argued that flightlessness in birds and insects would be lost after a species had colonised an island as during flight individuals would risk being blown out to sea. Work by Cody & Overton (1996) and Fresnillo & Ehlers (2008) tests the same idea for plants and clearly indicates that dispersal ability is reduced in long-established island populations compared to those of the same species on the mainland. In other studies, the same mechanism has been invoked as an explanation for reduced dispersal ability of plants growing in fragmented landscapes (Cheptou *et al.*, 2008; Riba *et al.*, 2009). Importantly, Cheptou *et al.* (2008) and Riba *et al.* (2009) both provide some initial evidence that the differences in dispersal between fragmented and contiguous populations have a heritable component.

The opposing selective pressure that favours longer-distance dispersal comes from the advantage that is gained if a plant's seeds are amongst the first to colonise an empty patch. They benefit from the low interspecific competition that is found there and can experience rapid population growth. The offspring of these patch colonisers will themselves have good dispersal ability and thus will have higher chances of reaching other patches. In a system where there is stochastic extinction of local populations, the importance of having dispersal strategies that enable colonisation can override the importance of not dispersing too many seeds into the inhospitable matrix and higher dispersal distances can evolve. This is exactly what we observe; when we introduce stochastic patch extinctions we obtain an increase in release height. It is worth noting that risk spreading provides another mechanism that also promotes increased dispersal under temporally variable environments (e.g. Kisdi, 2002).

While evolutionary suicide and evolutionary rescue effects have been shown before in relation to dispersal, it has typically been demonstrated in highly theoretical often mathematical

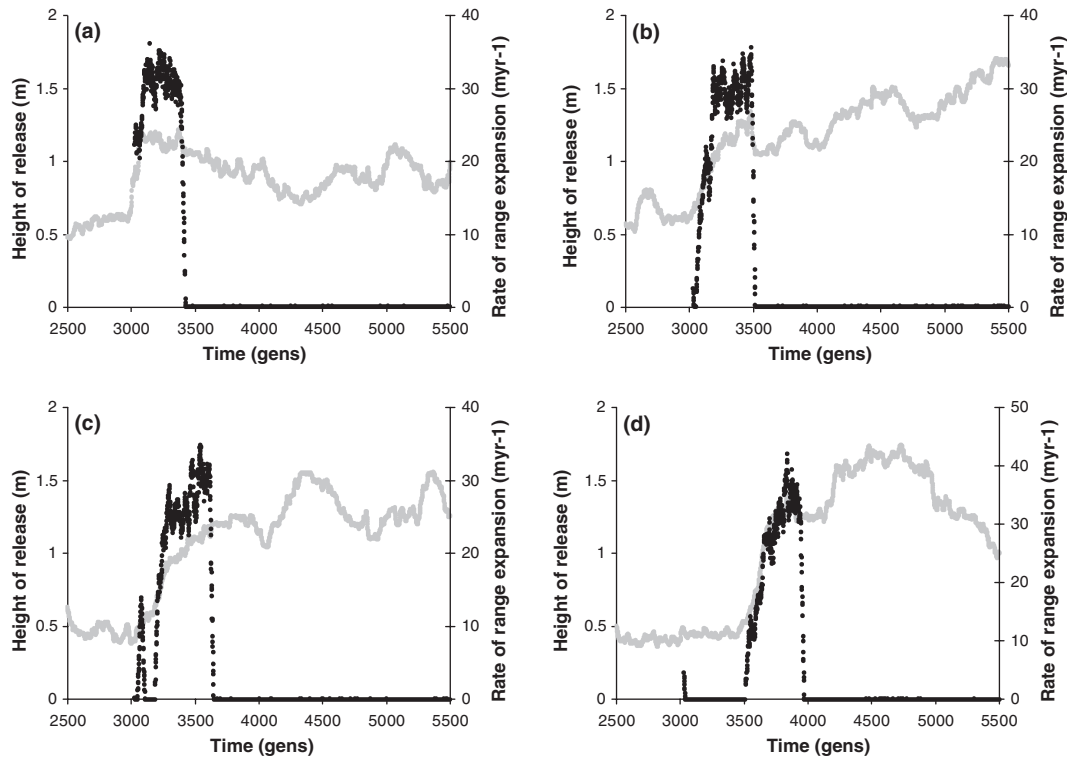


Figure 6 Evolution of increased release height accelerates range expansion. Here we show four examples where range expansion is allowed to occur from time = 3000. In all cases the model is run using identical parameters (700 patches of radius 10 on a landscape with dimensions 12,000*100. $c = 20.0$, initial height = 0.5) and the differences between the runs exemplify both the stochasticity and complexity present in the results. Mean height of release is shown in grey and rate of spread in black. In all four examples there is an increase in release height during the early stages of expansion and this leads to acceleration in range expansion. In some cases initial expansion is relatively fast (a) and the increase in rate of spread because of evolution is less. However, in the main, we see substantial acceleration (b–d). In some cases, during the initial expansion, the population’s spread can be temporarily ‘blocked’ by a gap in the landscape until a sufficiently dispersive genotype emerges (c, d). In the example in d the population is trapped for 500 generations but once it escapes height of release rapidly evolves upwards. In most cases we do not observe a rapid return to pre-expansion release height after the population has filled the landscape and spread has ceased (this occurs around gen = 3500 in a, b, gen = 3700 in c and gen = 3950 in d).

models (e.g. Gyllenberg *et al.*, 2002; Heino & Hanski, 2001; Rousset & Ronce, 2004). Our results suggest that the effects are robust to the addition of increased biological realism and we anticipate that they are likely to be important real effects in plant populations. One important point that we want to stress here is that even when we run repeat simulations for the same parameter values we sometimes observe rescue effects and sometimes suicide. This highlights the stochasticity involved and indicates that it may often be hard to predict the outcome. We suggest that a pragmatic recommendation would be that following a period of rapid habitat loss and fragmentation, as well as monitoring population size and patch occupancy, life history traits related to dispersal should be monitored. This would serve to provide an early warning that evolutionary suicide might be occurring. Additionally, it is worth considering whether conservation strategies should include artificial selection to promote more dispersive characteristics thus increasing the chances that a rescue trajectory rather than a suicide trajectory is followed by the population.

We have observed some examples where there appear to be cyclic dynamics in release height and patch occupancy (e.g.

Fig. 4d). We have not run sufficient simulations to confirm the existence of, or the mechanism behind, this pattern. However, we believe it is a potentially very interesting effect deserving of further attention in future work. We speculate that the following may be behind the observations. Initially, release height is low, and this results in low patch occupancy. However, selection can favour increased release height as this increases the chances of seeds reaching empty patches where they and their progeny can exploit plentiful resources. As release height evolves upwards, patch occupancy gradually increases. When the landscape is saturated, there is no longer as great a benefit of reaching other patches. Even if a patch suffers a disturbance that kills all the individuals, it is likely that more than one seed will rapidly reach it and thus the benefit of being a coloniser is lowered. Under these conditions, balance between the two selective forces will switch back to that favouring lower dispersal to minimise loss of propagules to the matrix. Over time, this can then lead to a reduction in the populations’ ability to colonise empty patches, patch occupancy will decline and the situation is back to where it was at the start with low release height and low patch occupancy.

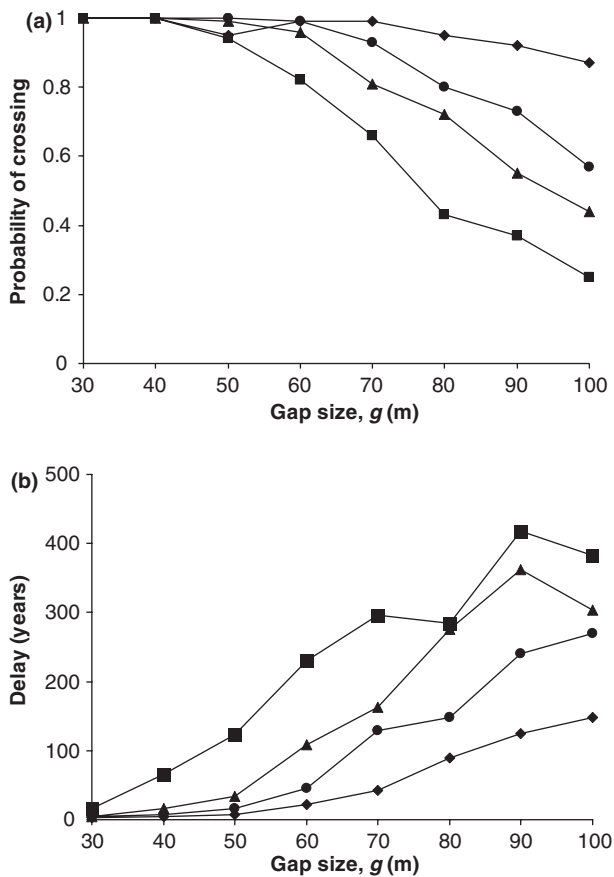


Figure 7 Evolutionary entrapment is most likely when an unusually large gap occurs soon after a species has started expanding its range. The probability that the larger gap is crossed at any time during the simulation is shown in (a) (each simulation lasts a maximum 1000 years). Even in simulations where the larger gap is eventually crossed there can be a substantial delay to range expansion. This delay to range expansion depends upon the size of the gap and where it occurs (b). In both a and b, diamonds show results for $P = 20$ (i.e. when the larger gap is encountered after 20 patches), circles show results for $P = 40$, triangles $P = 60$ and squares $P = 100$.

And, under these conditions, there can again be a change in the balance between selective forces that will drive up release height and start the cycle again. We only occasionally observe dynamics that appear cyclic and suggest that one possibility may be that whether or not they occur may depend upon the particular spatial arrangement of patches on the landscape.

There has been much recent interest in the evolutionary dynamics of range expansion (e.g. Excoffier *et al.*, 2009; Burton & Travis, 2008) and there is good evidence that dispersal can be selected upwards at expanding range margins (e.g. Phillips *et al.*, 2006; Cwynar & MacDonald, 1987 and Darling *et al.*, 2008). Theoretically, this empirical observation is well understood (Travis & Dytham, 2002); at an expanding front, those individuals (and their descendants) possessing greater dispersal ability are more likely to benefit from the low densities at the front. The descendants of less dispersive individuals are

unlikely to keep pace with the front. In our model, we often observe a substantial increase in release height in range expanding populations and a consequence of this is a rapid increase in the rate of range expansion. Previous models investigating dispersal evolution during range expansions (Travis & Dytham, 2002; Travis *et al.*, 2009) have used nearest-neighbour dispersal. In these models, there was at most around a two-fold increase in the rate of range expansion because of dispersal evolution. Here, we regularly see much greater acceleration in rate of expansion (increases from under 1 m yr^{-1} up to 40 m yr^{-1} in some cases) and this serves to emphasise the importance of considering the evolution of dispersal kernels in future work.

During our initial simulations of range expansions, we sometimes observed that populations seemed to be become trapped and this seemed to occur when unusually large gaps between habitat patches impeded spread (examples in Fig. 6). Experiment 3B was designed to explore this effect in greater detail. The results of this experiment (Fig. 7) illustrate that the entrapment is not simply ecological in nature. Instead, it is much more likely to occur in the early stages of invasion before selection has had a chance to increase dispersal distance (in our case through increasing release height). However, if there is sufficient, well-connected habitat prior to a large habitat gap, then there is a much better chance that evolution will have resulted in the invasion having acquired sufficient speed (through greater dispersal distances) that it is able to successfully (and rapidly) jump across the gap.

We have introduced a model for dispersal evolution in plants where dispersal is modelled mechanistically, and the evolution of the dispersal kernel results from selection acting on the height at which seeds are released. We have run the model for a few scenarios of conservation relevance to illustrate the types of effect that may be observed. We believe that by adding biological realism to models that incorporate evolution we can move beyond abstract theory towards directly conservation relevant models. Clearly, this is just a start and much further work is required. For example, a plant's dispersal kernel will depend upon factors other than release height. Terminal velocity and abscission thresholds will also be important and future models could usefully incorporate evolution of these traits. An interesting question for future work will be what shapes of dispersal kernel typically emerge from the evolution of one or more traits in the type of evolutionary, mechanistic model that we have presented a first example of here. A further challenge in running continuous space models for plants will be defining the competition kernel. Empirical work seeking to establish the shape of these kernels and theoretical work exploring the potential role of the competition kernel in driving the evolution of dispersal would both be interesting avenues to explore.

As we develop these more complex models, we will require greater information for parameterisation if they are to be used tactically. Trade-offs will be important and we will need empirical information on the nature of key trade-offs (for example seed number versus release height). Most previous

theory on dispersal evolution has not explicitly accounted for trade-offs and extensions of the modelling described here could ask how important the presence (and nature) of a trade-off is in determining the evolutionary and ecological dynamics that emerge. In this paper, we have chosen to assume a simple trade-off between seed production and release height. In reality, the relationship will not always be straightforward; for example, plants in good conditions may both grow taller and produce more seeds, or plants with higher flower stalks may set more seed because they are more visible to pollinators. Complexities such as these mean that it will be a considerable challenge to move from the still quite abstract model presented here towards predictive species-specific models. However, we believe that by extending our approach, it will be possible to gain increased insights into several important questions related to, for example, the within and between species variability in plant heights. A further critical issue is that, if we are to be able to predict the time frame over which evolutionary effects will occur, we will need information on the heritability of traits and their genetic architecture. While developing evolutionary models to be used as conservation tools is undoubtedly a challenge, we believe that, with a concerted collaborative effort linking the knowledge and methods of ecologists, evolutionary biologists and geneticists, it is an achievable aim. Our hope is that moving from abstract, highly theoretical models to more complex, but biologically realistic models can be an important first step.

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