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1 The evolution of density dependent dispersal during a range expansion  
2 leads to substantial emigration below equilibrium density, accelerating  
3 the invasion rate.

4

5

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14

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17

18 Running title: Evolution of dispersal during range expansions.

19

20 Key words: lifetime reproductive success, fitness, climate change, invasion, migration

21

## 1 **Summary**

2 Evolutionary processes play an important role in shaping the dynamics of range  
3 expansions, and selection on dispersal propensity has been demonstrated to accelerate  
4 rates of advance. Previous theory has considered only the evolution of unconditional  
5 dispersal rates, but dispersal is often more complex. For example, many species  
6 emigrate in response to crowding. Here, we use an individual-based model to  
7 investigate the evolution of density dependent dispersal into empty habitat, such as  
8 during an invasion. The landscape is represented as a lattice and dispersal between  
9 populations follows a stepping-stone pattern. Individuals carry three 'genes' that  
10 determine their dispersal strategy when experiencing different population densities.  
11 For a stationary range we obtain results consistent with previous theoretical studies:  
12 few individuals emigrate from patches that are below equilibrium density. However,  
13 during the range expansion of a previously stationary population, we observe  
14 evolution towards dispersal strategies where considerable emigration occurs well  
15 below equilibrium density. This is true even for moderate costs to dispersal, and  
16 always results in accelerating rates of range expansion. Importantly, the evolution we  
17 observe at an expanding front depends upon fitness integrated over several  
18 generations and can not be predicted by a consideration of lifetime reproductive  
19 success alone. We argue that a better understanding of the role of density dependent  
20 dispersal, and its evolution, in driving population dynamics is required especially  
21 within the context of range expansions.

22

23

24 Key words:

25 Dispersal, Evolution, Invasion, Range shifting, Climate change, Exotic

## 1 **Introduction**

2 Dispersal plays a central role in a population's ecological and evolutionary dynamics  
3 (Bowler and Benton 2005). Dispersal influences spatial population dynamics (Kendall  
4 et al. 2000; Paradis et al. 1999); for example it can determine the probability of  
5 persistence (Brachet et al. 1999; Johst et al. 2002), and influence the rate at which  
6 populations expand their ranges (Neubert and Caswell 2000). Additionally, it can  
7 shape community structure (Levine and Murrell 2003), and at a broader spatial and  
8 hierarchical scale can determine species' biogeographic ranges (Brown et al. 1996).  
9 Evolutionarily, dispersal determines the extent, and direction, of gene flow between  
10 different parts of the population or between populations within a metapopulation.  
11 Gene flow, in turn, influences the degree to which populations become locally  
12 adapted (Alleaume-Benharira et al. 2006). Dispersal may also lead to evolutionary  
13 effects at the macroecological scale: for example, theory has demonstrated that  
14 relatively frequent, large scale dispersal can potentially place limits on a species'  
15 biogeographic range (Kirkpatrick and Barton 1997) by restricting the ability of a  
16 species to adapt to more marginal conditions. Dispersal can itself be labile, and its  
17 evolution has been the topic of considerable theoretical and empirical interest (e.g.  
18 Bowler and Benton 2005). There is an expectation that the availability of suitable  
19 habitat for species will change with global climate change (Ohlemüller et al. 2006;  
20 Thuiller et al. 2005). In such cases, as with species introduced into new areas, the  
21 species can undergo a range expansion into the previously unoccupied, but now  
22 suitable, habitat. Here, we are interested in understanding how dispersal is likely to  
23 evolve in populations undergoing range expansions, and also ask how evolution  
24 affects the rate of that range expansion.

25

1 Given the increasing attention devoted to the consequences of dispersal, it is  
2 unsurprising that there has been considerable recent interest in bettering our  
3 understanding of what determines different dispersal strategies (e.g. Cadet et al. 2003;  
4 Poethke and Hovestadt 2002; Travis and Dytham 2002; see Bowler and Benton 2005  
5 and Ronce 2007 for reviews). Dispersal carries several potential costs that together  
6 offset the benefits and therefore place a limit on its evolution. There may be  
7 considerable energetic costs associated with movement between patches (Stobutzki  
8 1997; Zera and Mole 1994) and predation risk may be higher for dispersers than non-  
9 dispersers (Bélichon et al. 1996; Yoder et al. 2004). Also a dispersing individual may  
10 move to an unsuitable location. Despite these costs, dispersal is ubiquitous. This is  
11 due to several strong selective forces that act to favour movement of individuals  
12 between patches. Dispersal becomes increasingly favoured as temporal environmental  
13 variability (McPeck and Holt 1992; Travis 2001) and/or demographic stochasticity  
14 (Travis and Dytham 1998; Cadet et al. 2003) increase. Dispersal enables regional  
15 population persistence despite the frequent local extinctions that both high temporal  
16 environmental variability and demographic stochasticity can generate (Metz and  
17 Gyllenberg 2001; Olivieri et al. 1995; Parvinen et al. 2003). Selection can also favour  
18 dispersal as it reduces both kin competition (Bach et al. 2006; Gandon 1999; Ronce et  
19 al. 2000) and inbreeding (Gandon 1999; Motro 1991; Perrin and Mazalov 1999).

20

21 During periods of range expansion, selection pressures on dispersal can be very  
22 different to those on individuals in a stationary population. At an expanding margin,  
23 there will generally be strong selection favouring increased dispersal, as there are  
24 considerable fitness benefits of being amongst the earliest colonists of a new patch.  
25 This is both predicted by theoretical models (e.g. Phillips et al. 2008; Travis and

1 Dytham 2002), and observed to be the case in invasive species (e.g. Phillips et al.  
2 2006) and in populations undergoing range expansions in response to climate change  
3 (e.g. Hughes et al. 2003; Simmons and Thomas 2004). Interestingly, the evolution of  
4 increased dispersal at range margins can be severely limited for populations  
5 experiencing Allee effects (Travis and Dytham 2002). We know that many, and  
6 perhaps most, animal species exhibit density dependent dispersal (e.g. Denno and  
7 Peterson 1995; Matthysen 2005). However, with some exceptions (Bach et al. 2007;  
8 Kun and Scheuring 2006; Poethke and Hovestadt 2002; Travis et al. 1999), the great  
9 majority of models focussing on dispersal evolution have, in common with most  
10 theory on spatial populations, modelled the evolution of density independent rates of  
11 movement between patches (Bowler and Benton 2005). Understanding the evolution  
12 of density dependent dispersal may be particularly important for populations  
13 undergoing range expansions as towards the advancing front individuals may  
14 frequently be at much lower densities than they would typically be found within  
15 stationary ranges. We take advantage of recent developments in modelling density  
16 dependent dispersal strategies (Kun and Scheuring 2006) to consider how emigration  
17 strategies may evolve in periods of range shifting.

18

## 1 **The Model**

2  
3 We develop an individual-based, spatial simulation model to investigate the evolution  
4 of density dependent dispersal during invasions. Simulations take place in an arena of  
5 cells (dimensions  $x=700$  and  $y=20$ ) and the model runs in discrete time. The modelled  
6 population expands in the  $x$ -dimension hence we use a lattice that is much longer than  
7 it is wide. In the following sections we consider in more detail how the within-  
8 subpopulation dynamics and dispersal are modelled, and then describe the simulation  
9 experiments.

### 11 **Within-subpopulation dynamics**

12 Within-subpopulation dynamics are described by an individual-based formulation  
13 based on Hassell and Comins (1976). Each individual in the subpopulation at time  $t$   
14 gives birth to a number of offspring drawn at random from a Poisson distribution with  
15 mean  $\mu$  defined as

$$16 \mu = \lambda(1 + aN_t)^{-b}$$

17 Here,  $\lambda$  specifies the intrinsic rate of increase,  $a$  relates to patch quality and  $b$   
18 describes the type of competition. When  $b=1$  the competition is ‘contest’ and as  $b$   
19 increases, the nature of the competition becomes increasingly ‘scramble’. The  
20 parameter  $a$  is calculated from the following expression:

$$21 a = (\lambda^{1/b} - 1) / N^*,$$

22 where  $N^*$  is the subpopulation equilibrium density. Drawing the number of offspring  
23 born to each adult from a Poisson distribution introduces demographic stochasticity  
24 into the model (Poethke and Hovestadt 2002; Travis and Dytham 1998, 2002).



1           The density dependent dispersal strategy of each offspring is determined by  
 2 three parameters ( $D_0$ ,  $\alpha$ , and  $\beta$ ) that are controlled by their inherited dispersal  
 3 genotype, with small, independent probabilities of mutations,  $m_d$ ,  $m_\alpha$  and  $m_\beta$  (see  
 4 dispersal section below). We model haploids with asexual reproduction. In all the  
 5 results presented here  $m_d$ ,  $m_\alpha$  and  $m_\beta = 0.001$ . When a mutation occurs the new value  
 6 of the parameter is modified by a value drawn from the following uniform  
 7 distributions:

8 For  $D_0$ : -0.1 to 0.1 (with resulting value constrained to  $0.0 < D_0 < 1.0$ )

9 For  $\alpha$ : -0.5 to 0.5 (with resulting value constrained to  $0.0 < \alpha < 10.0$ )

10 For  $\beta$ : -5.0 to 5.0 (with resulting value constrained to  $\beta > 0.0$ )

11

12 For comparison, we run some simulations where dispersal is density independent. In  
 13 these simulations individuals carry just a single parameter that determines their  
 14 dispersal probability. When a mutation occurs to this parameter it is modified by  
 15 +/- 0.1 with the resulting value constrained to between 0.0 and 1.0.

16

17 All individuals die as soon as they have reproduced.

18

## 19 **Dispersal**

20 Dispersal occurs immediately after the within-population dynamics. Individuals  
 21 disperse with probability  $d$ . In the cases where density dependent dispersal is  
 22 employed, the probability of emigration is described by the following equation:

$$23 \quad d = \frac{D_0}{1 + \text{Exp}[-(N(x, y) - \beta) \cdot \alpha]}$$

24 This is dependent on the strategy of the individual and the local population density,  
 25  $N(x, y)$ . The function used to describe density dependent dispersal is very flexible and

1 can describe a multitude of potential strategies (see Figure 1, and also Kun and  
2 Scheuring (2006) for more examples).  $D_0$  is the maximal dispersal probability,  $\beta$  is the  
3 inflection point of the function, and  $\alpha$  determines the sharpness of the increase at the  
4 inflection point. In the simulations where dispersal is density independent,  
5 individuals carry just one parameter that directly determines their probability of  
6 dispersal,  $d$ . The cost of dispersal is represented as the probability of mortality  $c$ , and  
7 those that survive move with equal likelihood to one of the nearest eight patches  
8 (Moore neighbourhood). We assume that individuals dispersing off the edge of the  
9 lattice die (absorbing boundary conditions).

10

### 11 **Simulation experiments**

12 Unlike the similar model of density dependent dispersal presented in Kun and  
13 Scheuring (2006), we do not follow the adaptive dynamics framework (Dieckmann  
14 and Ferrière 2004). In our artificial world multiple strategies can be present, and  
15 competing.

16 We first run a set of simulations for a stationary population to establish whether the  
17 results produced from our model are qualitatively similar to those described by Kun  
18 and Scheuring (2006). In these simulations the model runs on a 20 by 20 lattice for  
19 10000 time steps and we track the evolutionary dynamics of the three parameters that  
20 together determine the shape of the dispersal function. 10000 time steps is ample time  
21 for the population to reach an equilibrium strategy regardless of the initialisation of  
22 the three labile parameters.

23

24 We next consider how the dispersal strategy evolves when the population is allowed  
25 to expand its range into a new region. In these simulations the model is run for 15000

1 time steps on a 20 row by 700 column lattice. For the first 10000 time steps the  
2 population is constrained to the first 20 columns, with the 21<sup>st</sup> column acting as an  
3 absorbing boundary. Beyond 10000 generations, the whole lattice is available for  
4 occupation, and the population is able to extend its range. In these simulations we  
5 track both the evolution of the three parameters at the expanding front and the rate at  
6 which the range expansion occurs. To obtain the strategy of the expanding front  
7 population we identify all those individuals that are within five columns of the  
8 expanding range. In all cases we run the model 20 times for each parameter  
9 combination and we calculate means and 95 confidence intervals for those 20  
10 repetitions.

11

## 12 **Results**

13 In a stationary population selection is strongest on  $\beta$ , the parameter controlling the  
14 position of the threshold local abundance, below which there is little dispersal (Figure  
15 2). Selection favours individuals that have  $\beta$  values close to the equilibrium density,  
16  $K$ . Selection also acts rapidly on  $D_0$ , the parameter controlling the maximum dispersal  
17 probability from a patch (the asymptote of the function). Selection acts less strongly  
18 on the steepness of the transition from low to high dispersal close to  $K$ , and so the rate  
19 at which  $\alpha$  approaches an equilibrium is much slower (Figure 2). Frequency  
20 distributions of individuals carrying genes for different values of the three parameters  
21 indicate that at any one point in time there is a spread of strategies within the  
22 population, and this is maintained by a mutation-selection-drift balance (Figure 3).

23

24 During a period of range expansion, we frequently observe rapid change in the density  
25 dependent dispersal strategy. At the range front, the mean of one or more of the three

1 parameters shifts substantially during a period of expansion (Figure 4) and this leads  
2 to an acceleration in the rate of expansion (Figure 5). Interestingly, it is not always the  
3 same parameter that shows the greatest change at the expanding front. Three  
4 independent simulations of the model with identical parameter values are shown in  
5 Figure 4, and while in two of the three simulations (grey symbols) the greatest change  
6 at the front is in  $\beta$ , in the third (black) it is  $\alpha$ , and in this case there is little evolution in  
7  $\beta$ . In both cases the *evolution results in a strategy where dispersal occurs even at*  
8 *very low densities*. After the population has fully occupied the lattice, (at around  
9 time=12300 in the simulations presented here - Figure 5), the whole population  
10 gradually evolves back towards the dispersal strategy that is selected in a stationary  
11 population (Figure 4). This return to a stationary strategy happens less rapidly than the  
12 switch to an expansion strategy observed at the start of range shifting. A key feature  
13 of the results is that individuals at the front are selected to disperse at much lower  
14 local densities than those in stationary populations. As the front moves away, there is  
15 a gradual shift in strategy such that individuals become much less likely to disperse at  
16 lower local population density, and ultimately the strategy will return to that found in  
17 the initial stationary population.

18

19

20 Where dispersal is density dependent we observe a greater acceleration in range  
21 expansion due to dispersal evolution (2.2 times faster than in the stationary  
22 population) than if it is density independent (1.4 times faster) (Figure 6). This is true  
23 regardless of the cost of dispersal. Whatever the form of dispersal, increased costs  
24 result in reduced rates of spread both before and after evolution. In the case of density  
25 independent dispersal the acceleration in range expansion shown in Figure 6 is due to

1 the evolution of the single parameter controlling the probability that an individual  
2 disperses. Across the whole range of dispersal costs investigated, the probability of  
3 dispersing evolves to substantially higher values at the expanding front following a  
4 period of range expansion (Figure 7A). It is interesting to note that even when half of  
5 all dispersing individuals die, there is a four-fold increase in dispersal probability  
6 from 0.05 to 0.20. When the evolution of the density dependent strategy is considered,  
7 three parameters can evolve. All three parameters do come under selection during a  
8 period of range expansion.  $D_0$ , the asymptote of the relationship, tends to evolve  
9 upwards (Figure 7B), while much lower values of  $\beta$  are selected (Figure 7C). This  
10 evolution towards lower  $\beta$  brings the inflexion point of the relationship closer to the  
11 origin. On average there is also selection for lower values of  $\alpha$  (Figure 7D), which  
12 leads to a more gradual increase in dispersal probability around the inflexion point. As  
13 highlighted earlier, and shown in Figure 4, each of the three parameters may or may  
14 not evolve in any one simulation, and in fact a fairly rapid change in either, but not  
15 both,  $\alpha$  or  $\beta$  is often observed. In the simulations presented here,  $\beta$  tends to evolve to  
16 lower values more often than does  $\alpha$ , and a more gradual increase in  $D_0$  occurs fairly  
17 consistently across simulations. These patterns are maintained across the range of  $c$   
18 investigated.

19  
20 The dispersal strategy that evolves during range expansion is remarkable in that it  
21 leads to dispersal at low densities. This is surprising because within low-density  
22 patches resources are available, so there are benefits to not dispersing, while dispersal  
23 can carry several different costs. Consider an individual in a patch on its own at the  
24 range front. The individual could not have a higher expected lifetime reproductive  
25 success than it would possess by staying put. By dispersing from this patch the

1 individual's expected lifetime reproductive success will be reduced for two reasons.  
2 First, because there is a cost of dispersal (probability of mortality), and second,  
3 because the direction of movement is random, it is equally likely that the individual  
4 will move in the opposite direction to which the range is expanding, and therefore in  
5 to a higher density patch, where it will suffer from greater competition. Thus the  
6 benefit of maintaining a position close to the range front must carry very substantial  
7 multigenerational benefits as despite these individual fitness costs, selection favours  
8 moderate levels of emigration even at very low local density.

9  
10 To confirm the importance of this multigenerational selection effect we ran two  
11 additional sets of simulations. In the first a population of individuals with an identical  
12 stationary strategy ( $D_{\theta}=0.45$ ,  $\alpha=1.75$ ,  $\beta=23.0$ ) is allowed to expand its range. The  
13 mutation rate is set to zero and the other parameters are as in Figure 4. We select a  
14 single individual right at the range front and monitor the number of children,  
15 grandchildren and subsequent descendants. The second set is identical except that  
16 here we change the strategy of the single individual selected, such that it is consistent  
17 with that which evolved in an expanding population ( $D_{\theta}=0.6$ ,  $\alpha=2.1$ ,  $\beta=0.1$  – see the  
18 mid grey line in Figure 4). For each set we run 200 replicate simulations and we  
19 establish the mean number of descendents for each of the 24 generations following  
20 introduction. We find that on average at  $t+1$  and  $t+2$ , the stationary individuals have  
21 more descendents: the stationary strategy has an average of 1.29 children and 1.43  
22 grandchildren whereas the expanding strategy has 1.05 and 1.34 respectively.  
23 However, for great grandchildren ( $t+3$ ) and beyond the expanding strategy performs  
24 better. At  $t+3$ , the expanding strategy has 1.79 descendants compared to 1.54 for the

1 stationary strategy, while by t+20 this gap has widened substantially to 29.58 versus  
2 6.57.

3

#### 4 **Discussion**

5 There is an increasing recognition that evolutionary processes can play an important  
6 role in the biology of range expansions (see reviews by Hänfling and Kollmann 2002;  
7 Hastings et al. 2005; Lambrinos 2004; Lee 2002). Local adaptation (e.g. Hammershøj  
8 et al. 2006; Parker et al. 2003; Reznick and Ghalambor 2001) and hybridization (e.g. ;  
9 Bossdorf et al. 2005; Ellstrand and Schierenbeck 2000) have both been shown to be  
10 important in driving the dynamics of some expansions, as has the evolution of life-  
11 history characteristics such as selfing rates (Daehler 1998), resistance to herbivores  
12 (Garcia-Rossi et al. 2003) and dispersal (Phillips et al. 2006, 2008; Simmons and  
13 Thomas 2004). Here, we have extended previous theoretical work investigating the  
14 evolution of density independent dispersal during range expansions, to consider how a  
15 flexible density dependent strategy might evolve. Previous theory indicates that if  
16 dispersal probability is allowed to vary according to local density, then in stationary  
17 populations very little, or no, emigration will occur below the equilibrium density  
18 (Kun and Scheuring 2006; Poethke and Hovestadt 2002; Travis et al. 1999). Our  
19 results show that during range expansion, selection favours a strategy where moderate  
20 rates of dispersal occur, even at very low local density and that the evolution of a  
21 density dependent strategy leads to a much greater increase in the rate of range  
22 expansion than is found when dispersal is density independent. Given that many, if  
23 not most, organisms exhibit density dependent dispersal (e.g. Denno and Peterson  
24 1995; Matthysen 2005) it is important that future empirical studies establish how this  
25 more complex strategy might evolve during range expansions.

1

2 The selection, at an expanding front, of a strategy that results in emigration even at  
3 low densities provides a good example of evolution not maximising lifetime  
4 reproductive success (e.g. Benton and Grant 2000; Coulson et al. 2006; Metz et al.  
5 1992). Our results clearly indicate that at an expanding range margin a dispersal  
6 strategy with substantially higher lifetime reproductive success will not necessarily  
7 have as many descendants as one with a lower lifetime reproductive success. This has  
8 implications for how fitness should be measured in populations that have non-  
9 stationary ranges (or population dynamics, in general), as for a wide range of traits it  
10 is likely that maximising lifetime reproductive success will not necessarily be the  
11 strategy that promotes the continued spread of your descendants with the expanding  
12 range front. For example, at the expanding front the population is growing at a close  
13 to maximal rate as density dependence is very weak. Under these circumstances,  
14 reproducing earlier is more important than reproducing more but later in life. This has  
15 implications for the optimal measure of an individual's fitness during range  
16 expansions and relates to the recent debate on the relative merits of rate-insensitive  
17 measures, such as lifetime reproductive success, and rate-sensitive measures that  
18 account for the timing of reproductive events, such as  $\lambda_{ind}$  (e.g. Brommer et al. 2002).

19

20 It is not surprising that the evolution of a density dependent dispersal strategy should  
21 lead to a greater acceleration in range expansion than is found for a density  
22 independent strategy. The density dependent strategy that evolves in a stationary  
23 population results in very few individuals dispersing when population densities are  
24 low, as will be the case in most of the local populations at the range front. This  
25 strategy creates a lag between a patch being newly colonised and the local population



1 reaching a sufficient density for individuals to begin dispersing. Evolution of the  
2 strategy such that there is a moderate probability of dispersal, even at low densities,  
3 removes this lag effect and thus can make a major difference to the rate of range  
4 expansion. For density independent dispersal this lag effect does not apply. As far as  
5 we are aware, no empirical studies have considered how density dependent dispersal  
6 might evolve at range margins. Our results demonstrate the potential for the evolution  
7 of density dependent dispersal strategies to have a major impact on the dynamics of  
8 expanding ranges. Empirical studies are required to establish how important this  
9 effect is likely to be and for which groups of organisms. Without data of this kind,  
10 considerable uncertainties will remain in making predictions of the terminal velocity  
11 of species' range expansions.

12  
13 In recent years several different functions have been employed to model the evolution  
14 of density dependence in dispersal behaviour (Kun & Scheuring 2006; Metz &  
15 Gyllenberg 2001; Poethke & Hovestadt 2002; Travis et al. 1999). Qualitatively we  
16 anticipate that we would have obtained extremely similar results using any of these  
17 alternative methods. The key result is that in a stationary population, below  
18 equilibrium density, there is strong selection against dispersal, while some dispersal is  
19 favoured above equilibrium density. This same result has been obtained regardless of  
20 the function employed to model the density dependent response. Using the flexible  
21 function proposed by Kun and Scheuring (2006), we have found that during a period  
22 of range expansion moderate levels of dispersal are selected even at very low  
23 densities. Using the Poethke and Hovestadt (2002) function this would be captured by  
24 the evolution of the threshold below which no emigration occurs to a value  
25 approaching zero, while the two-parameter model used by Travis et al. (1999) would

1 evolve during range expansion such that the linear relationship intercepts the y-axis  
2 above the origin – potentially resulting in a very similar strategy to one that evolved  
3 using the flexible function in Fig 4D (black line). Until we have sufficient data on the  
4 density-dependence of dispersal for a range of species we will not know how  
5 biological constraints will restrict the range of shapes that the relationship might take.  
6 Thus, at present, a discussion over the precise choice of function to model the  
7 relationship is unlikely to be productive. Fortunately, regardless of the choice of  
8 function, models seem likely to yield qualitatively similar results.

9  
10 In common with almost all previous theoretical studies on the evolution of dispersal,  
11 this paper models the evolution of phenotype in a simple haploid system. This  
12 approach enables us to determine the evolutionary stable strategy under different  
13 conditions, but tells us little about how rapidly changes in strategy will occur in real  
14 populations when selection pressures alter. Recent theory has suggested that the  
15 population genetics of range expansions may be very different to those in stationary  
16 populations (e.g. Edmonds et al. 2004; Klopstein et al. 2006, McNerny et al. 2009)  
17 and has highlighted that drift and founder effects can result in mutations that occur  
18 towards a front sometimes reaching high spatial extent and abundance even when they  
19 are deleterious (Burton & Travis 2008a, 2008b ; Travis et al. 2007). Excoffier and  
20 Ray (2008) argued that as dispersal has been observed to evolve rapidly at expanding  
21 margin, “selection pressures for faster dispersal must be very strong to overcome drift  
22 at the front”. Incorporating the genetics underlying dispersal phenotypes will allow us  
23 to gain a much improved mechanistic understanding of dispersal evolution during  
24 range expansions and make it more likely that we will be able to predict the rate at  
25 which it will evolve. Until very recently, knowledge on the genetic determinants of

1 dispersal was virtually non-existent, but progress is being made in this area and a  
2 candidate locus controlling dispersal has been identified in the Glanville fritillary  
3 butterfly (*Melitaea cinxia*) (Haag et al. 2005). In another study, a single locus has  
4 been found to control the frequency with which winged morphs of the pea aphid are  
5 produced under different environmental conditions (Braendle et al. 2005). While this  
6 pea-aphid study focussed on abiotic environment dependent dispersal, it seems  
7 reasonable to anticipate that we will also find loci that control the propensity to  
8 disperse in relation to local biotic conditions. As contemporary genetic methods such  
9 as quantitative trait loci (e.g. Erickson et al. 2004; Mauricio 2001) increasingly reveal  
10 the mechanisms behind life history traits (Roff 2007) we need to develop a new  
11 generation of diploid genetic models incorporating recombination that explicitly  
12 model the genetic architecture responsible for characteristics such as dispersal.  
13 Combining the rich information now emerging from molecular studies with  
14 mechanistic evolutionary models has the potential to make theoretical evolutionary  
15 ecology a far more predictive discipline. In the meantime, we cannot say how  
16 “important” the evolution of density dispersal is in terms of the response of organisms  
17 in “ecological” or “societal” time scales (i.e. years to decades). However, there are  
18 many recent examples of evolution in ecological time (such as the age of maturation  
19 of fish under harvest) (Olsen et al 2004). In addition, the iterated founder effect at  
20 range margins may increase the potential rate of evolution markedly for populations  
21 with expanding ranges (McInerny et al 2009). Thus, there is now sufficient evidence  
22 to suggest the results presented here may be sufficiently important that they demand  
23 attention in the population management of species with expanding ranges.

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1 **Figure Legends.**

2 **Figure 1:** The flexible function used to describe density-dependent dispersal in the  
3 model. In (A)  $D_0 = 0.2$  (black line), 0.3 (mid grey) and 0.4 (light grey),  $\beta = 17$  and  $\alpha =$   
4 1.0. In (B),  $\beta = 10$  (Black line), 17 (mid grey) and 24 (light grey),  $D_0 = 0.4$  and  $\alpha =$   
5 1.0. In (C),  $\alpha = 0.25$  (black), 1.0 (mid grey) and 4.0 (light grey),  $D_0 = 0.4$  and  $\beta = 17$ .

6

7 **Figure 2:** Evolutionary trajectories of the three parameters in a stationary population.  
8 Here,  $K = 20$ ,  $\lambda = 1.5$ ,  $b = 1.0$  and the cost of dispersal,  $m = 0.1$ .

9

10 **Figure 3:** Mutation-selection equilibria for the three parameters at equilibrium. This  
11 highlights the difference between our approach which permits many strategies to be  
12 present at once within the population and the adaptive dynamics methodology adopted  
13 by Kun and Scheuring (2006) in which only two strategies, the resident and invader,  
14 are present at one time. These results are obtained for the same parameter  
15 combination used in Figure 2.

16

17 **Figure 4:** The evolution of dispersal strategy at an expanding range front. The  
18 population is allowed to expand its range at time=10000. The three grey shades show  
19 results for each of the three parameters for three representative runs of the model,  
20 using in each run the same parameter values ( $\lambda=1.5$ ,  $K=20$ ,  $m=0.1$ ). A-C show the  
21 trajectories of each of the three parameters involved. The solid lines in D show the  
22 strategies that results from evolution of those parameters. The values shown are the  
23 means for all those individuals within five patches of the expanding range limit. For  
24 comparison, the dashed line in D shows the strategy that evolves in a stationary range.

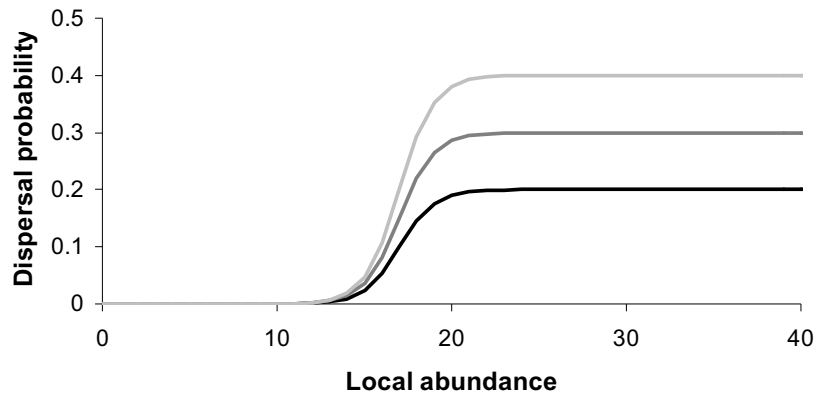
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1 **Figure 5:** Acceleration in range expansion due to evolution of the dispersal strategy.  
2 In black we illustrate the position of the range limit at the expanding margin. Range  
3 expansion begins at time=10000 and the whole landscape is filled by time=12300. In  
4 grey we show how the rate of range shifting varies through time. These data are  
5 generated using the same parameter values used for Figure 4.

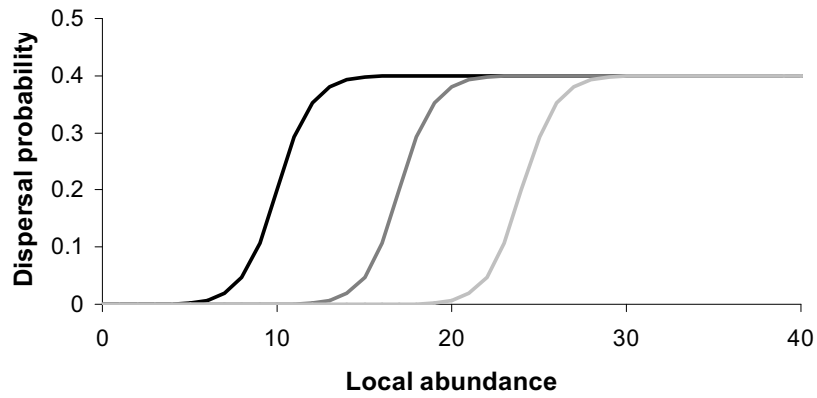
6  
7 **Figure 6:** the change in spread rate due to evolution of a density independent (A) and  
8 density dependent (B) dispersal strategy. In both, grey points show the rate of spread  
9 in the first 40 timesteps after the population is allowed to expand, while black points  
10 show the number of columns over which the population advances between 1460 and  
11 1500 timesteps after expansion started. In (C) these results are summarised by plotting  
12 the ratio of post versus pre evolution expansion rates for density independent (open  
13 squares) and density dependent strategies (black rhombuses). In all cases we display  
14 the means and 95% C.I.s for twenty runs of the model.

15  
16 **Figure 7:** Evolution of dispersal strategies for a range of dispersal costs. In A the  
17 probability of dispersal is shown for the density independent strategy while B-D show  
18 the evolution of the three parameters of the density dependent strategy. Grey points  
19 show the mean evolved strategy in a stationary population, while black points show  
20 the mean strategy of individuals within five columns of the leading edge of a range  
21 that has been expanding for 1500 timesteps. We plot the means and 95% C.I.s from  
22 20 runs of the model (in some cases the C.I.s are too small to be seen on the figure).  
23 Here,  $\lambda=1.5$  and  $K=20$ . For clarity, in D we show only the upper C.I. for the stationary  
24 population and only the lower C.I. for the range expanding population.

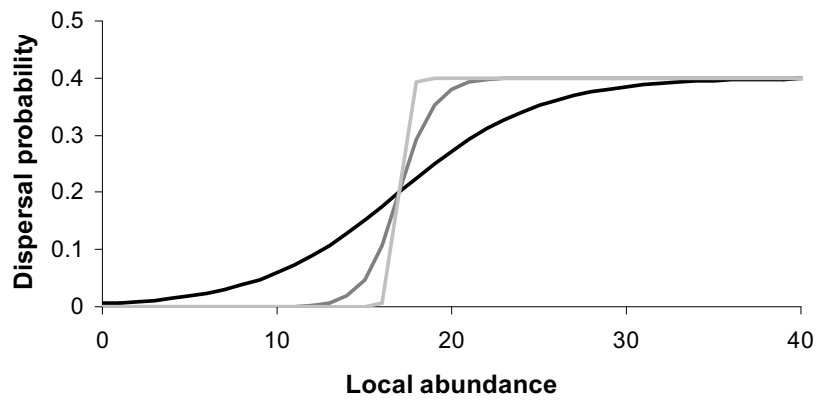
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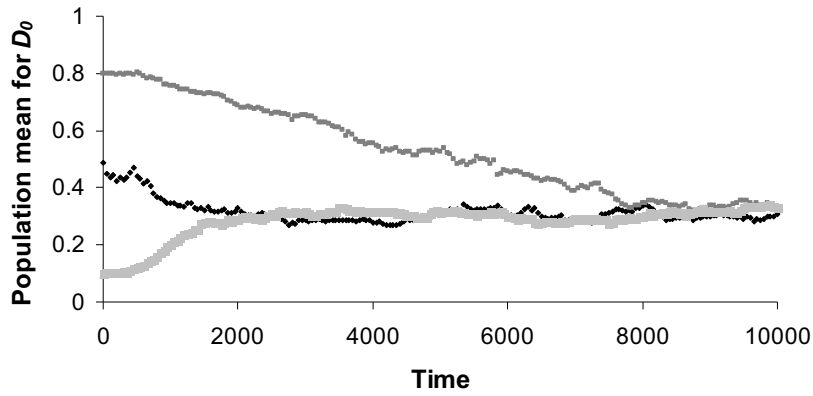


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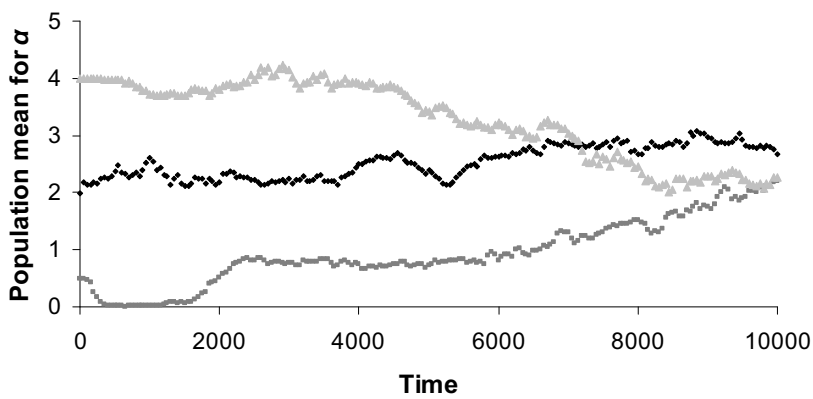
5 FIGURE 1

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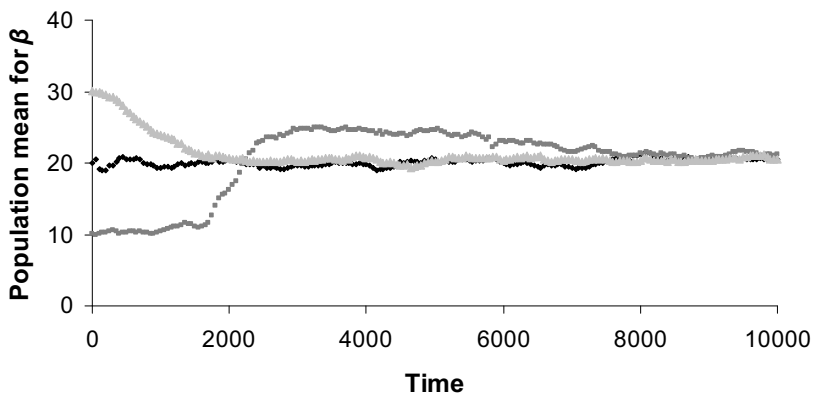
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4 FIGURE 2.

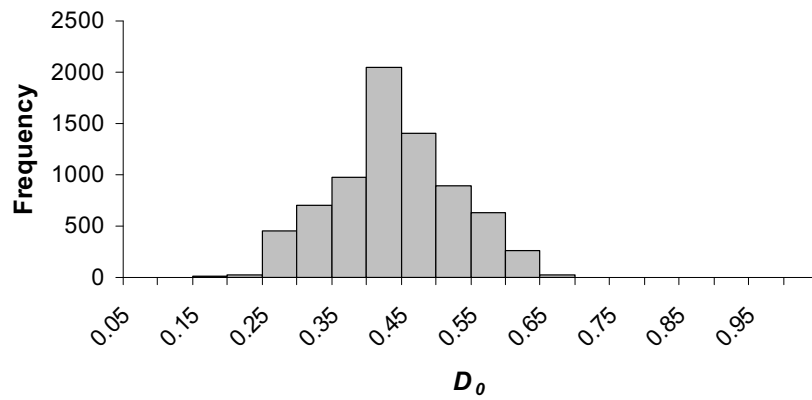
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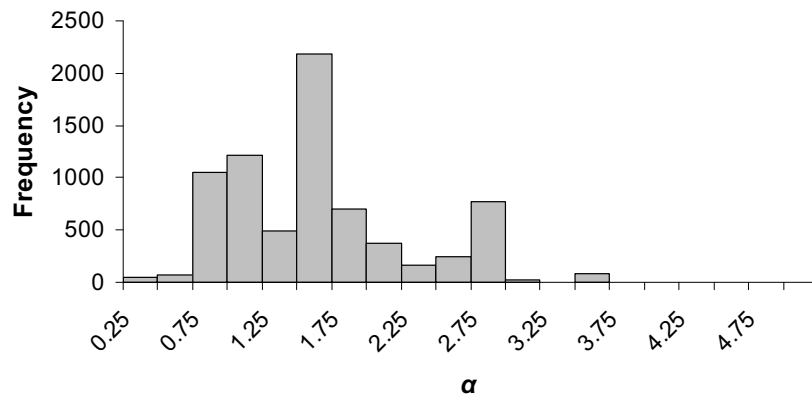
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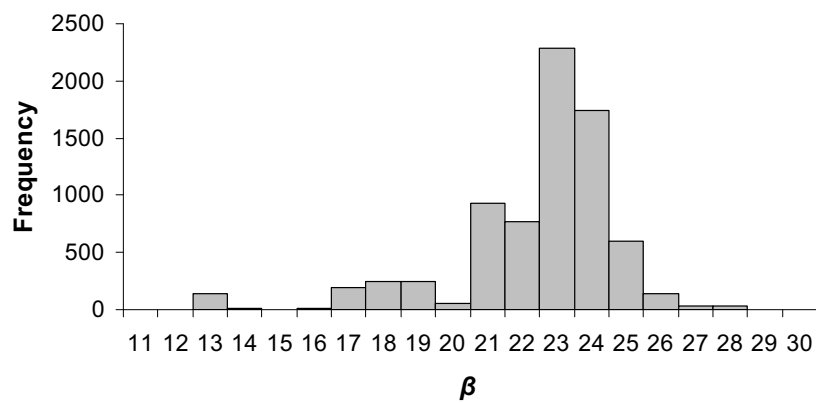
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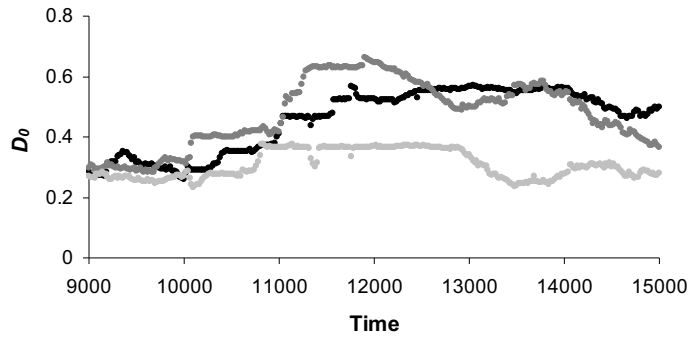


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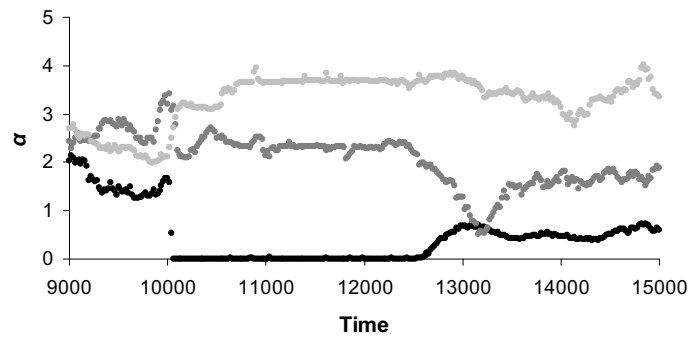
5 FIGURE 3.

6

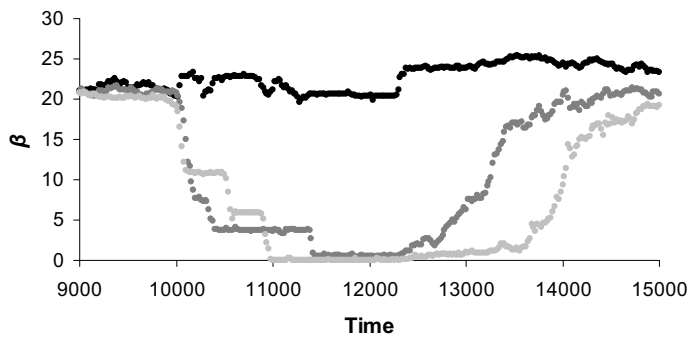
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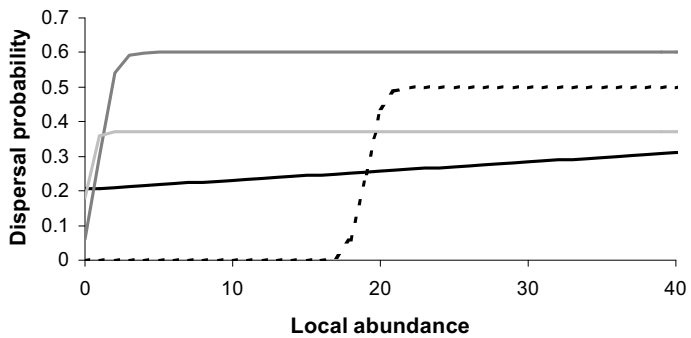
(A)



(B)



(C)



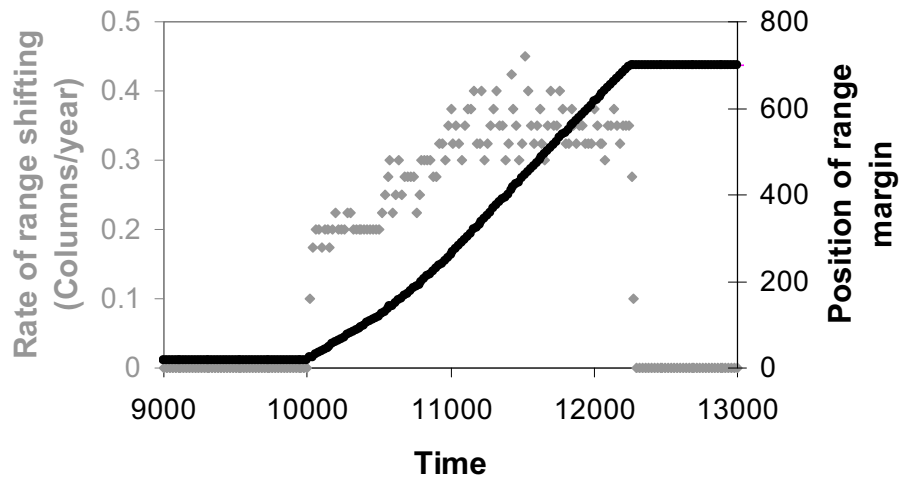
(D)

FIGURE 4

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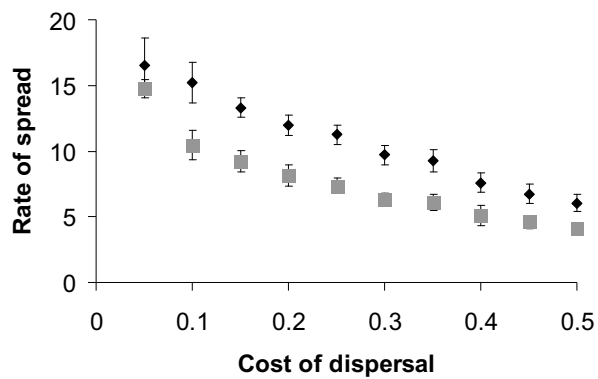
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3 FIGURE 5

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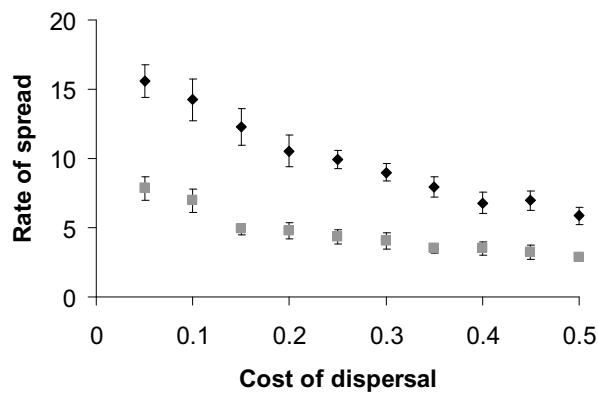
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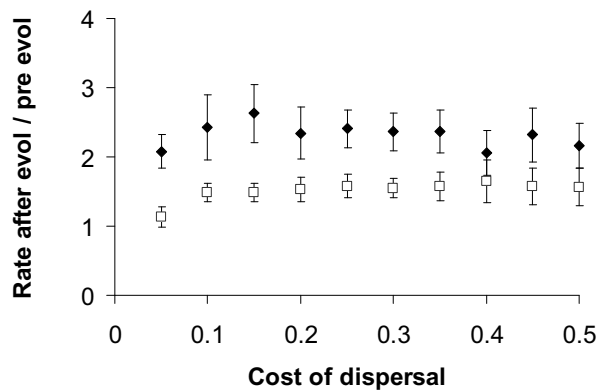
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6 FIGURE 6

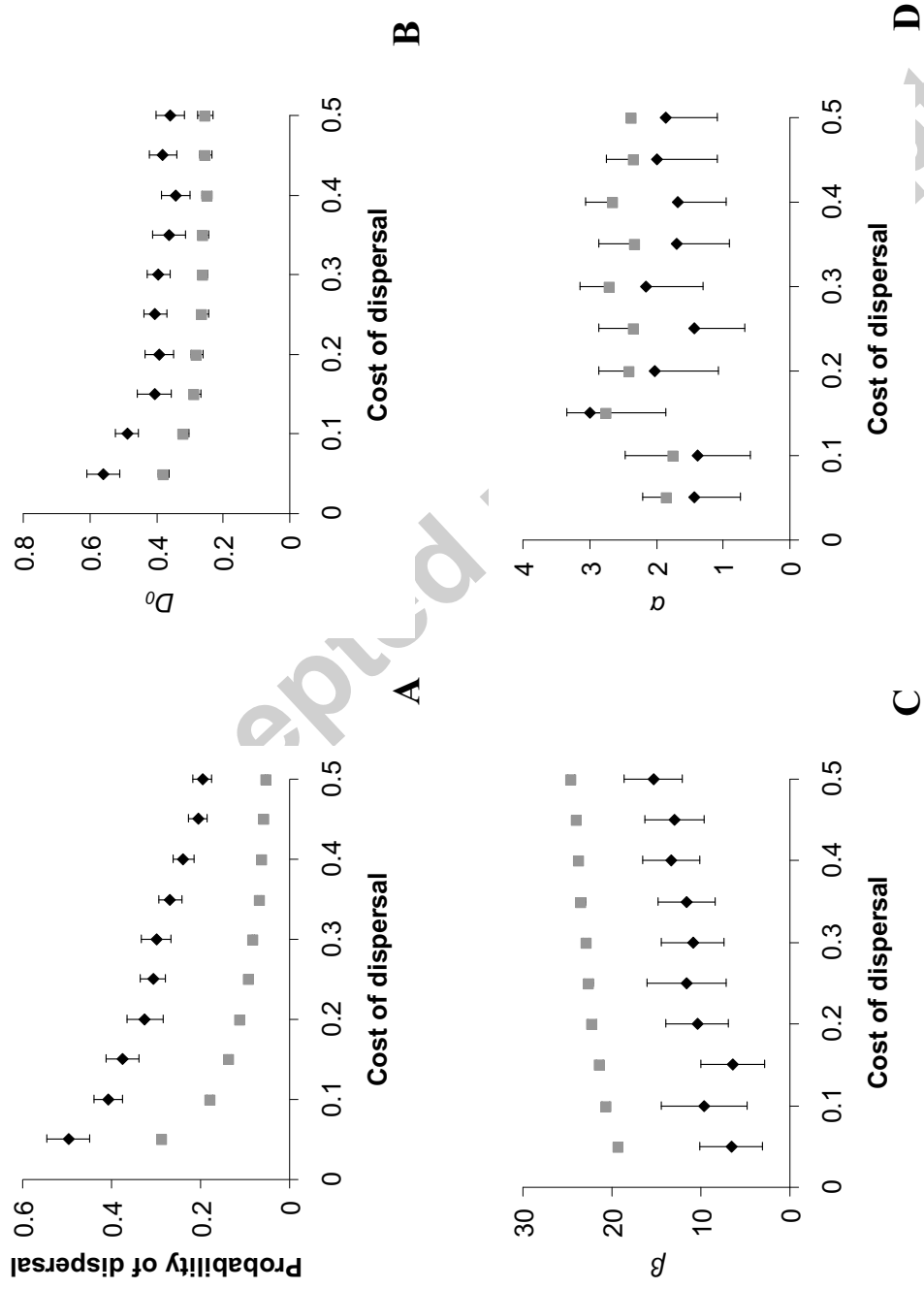
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FIGURE 7