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Evolution of density-dependent wing polymorphism in insects

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ABSTRACT

Questions: What are the conditions that lead to the evolution of density-dependent dispersal in wing-polymorphic insects?

Key assumptions: An asexual species whose eggs, larvae, and adult stages live in many patches. Within each patch, larval growth rate depends on the amount of renewable resources that are consumed by the larvae. Dispersal-type adults migrate out of the natal patch just before the reproductive stage. In contrast, reproductive-type adults are highly fertile but do not have the ability to disperse far. Genotypes differ in the way the fraction of the dispersal type responds to density during the larval stages. The carrying capacity of the resources fluctuates between high and low values.

Results: Density-dependent dispersal evolved if environmental fluctuation was high. The dispersal type was produced if the density exceeded a certain threshold, with the rate increasing as density increased. In contrast, no dispersal type evolved if environmental fluctuation was low. Also, the tendency for density dependence to evolve is enhanced by slow growth and fast mortality of larvae, high dispersal mortality, a rapid resource recovery rate, and rapid environmental fluctuation.

Keywords: density-dependent dispersal, environmental fluctuation, growth of insects, resource dynamics, wing polymorphism.

INTRODUCTION

Dispersal is widespread among organisms. It allows individuals to avoid unfavourable environmental conditions, such as kin competition (Hamilton and May, 1977), inbreeding (Motro, 1991), and depletion of resources due to high density. Temporal variations in the environment tend to select for dispersal (Roff, 1974a, 1974b; McPeek and Holt, 1992). The dispersal propensity of individuals is affected by habitat quality (McPeek and Holt, 1992), age (Ronce *et al.*, 1998), sex (Motro, 1991), body condition (Bonte and De La Pena, 2009), and parasite load (Iritani and Iwasa, 2014; Iritani, 2015). That dispersal propensity is sensitive to local density has been observed in a wide range of species (Denno *et al.*, 1991; Enfjall and Leimar, 2005; Meester and Bonte, 2010; Nowicki and Vravec, 2011).

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Theoretical studies have attempted to explain the relationship between density and dispersal rate as an outcome of evolution (e.g. Ezoe and Iwasa, 1997; Travis *et al.*, 1999; Poethke and Hovestadt, 2002; Amarasekare, 2004; Kun and Scheuring, 2006; Hovestadt *et al.*, 2010; Rodrigues and Johnstone, 2014). Most of these studies have reported the evolution of positive density dependence of dispersal, i.e. the rate of dispersal is greater at high density than at low density. However, when the temporal stability of the environment is increased, negative density dependence (i.e. the dispersal rate decreases with density) is observed (Rodrigues and Johnstone, 2014). Some of these studies assumed that dispersal rate is a function of density, and examined the evolution of parameters included in the functional form of dispersal rate (Travis *et al.*, 1999; Poethke and Hovestadt, 2002; Kun and Scheuring, 2006). For example, Travis *et al.* (1999) assumed that dispersal rate is a linear function of density and evaluated evolutionary dynamics using an individual-based model. Poethke and Hovestadt (2002) extended this research by assuming that the rate of dispersal is a non-linear function of density. In a coupled map lattice model, Kun and Scheuring (2006) investigated the evolution of costly dispersal.

In these studies, the population dynamics of the focal species was assumed to be dependent on density, and how resources affect individual growth rates was not considered. However, insects consume resources that are necessary for growth. In the present paper, we study a model for the evolution of density-dependent dispersal, incorporating the resource dynamics and growth process. We consider wing polymorphism in insect species with one of two wing types: the dispersal type, which has sufficiently strong wings for flight, and the reproductive type, which does not disperse far but has higher reproductive ability than the dispersal type (Roff, 1986; Denno *et al.*, 1989; Zera and Denno, 1997). Plant hoppers are insects that exhibit wing polymorphism: the wing type of plant hoppers is determined by population density during the larval stage. Larvae that experience a high density will develop into dispersal-type adults at a higher rate than will larvae that experience a low density (Kishimoto, 1956). Furthermore, the proportion of brachypterous individuals in a population and the effect of density on wing determination vary considerably among local populations (Iwanaga *et al.*, 1985; Denno *et al.*, 1991). Populations living in fluctuating environments produce more dispersal-type individuals (Denno *et al.*, 1991). These observations suggest that dispersal-type individuals are produced in a density-dependent manner, and the strength of the effect of density on wing determination is affected by the amount of environmental fluctuation experienced in the local environment.

In this paper, we study the evolution of wing determination in response to density during the larval stages. We show that density dependence changes with the amount of environmental fluctuation. We also assess how the parameters controlling resource dynamics and growth of organisms affect the determination of wing type.

THE MODEL

We consider an asexual population of insects living in a number of patches. The larvae grow in these patches from the egg to adult stage. There are two types of adults: the 'dispersal type' and the 'reproductive type'. Dispersal-type adults migrate out of the natal patch just before the reproductive stage, while reproductive-type adults, which are more fertile than the dispersal type, do not migrate. The density (per unit resource) encountered during the first to the third larval stage influences wing determination. In a low-density environment, all larvae grow to reproductive-type adults. However, if the larvae experience high density,

they mature into the dispersal type. As a consequence, the larvae mature into both dispersal-type and reproductive-type adults.

Stage-structured population

Figure 1 illustrates the life cycle of the insects. The number of developmental stages, i, takes a value from 1 to 5. The number of individuals in the ith stage is denoted by $N_{i,l}^{j}$, where the superscript j distinguishes between the 'dispersal type' ($j = 1$) and the 'reproductive type' ($j = 0$), and the second subscript l indicates the patch.

The dynamics of the number of eggs is represented as follows:

$$\frac{dN_{0,l}}{dt} = f^r N_{5,l}^r + mf^d (1/(l-1)) \sum\nolimits_{k \neq l} N_{5,k}^d \times (R_l/\bar{R}) - gR_l N_{0,l} - uN_{0,l}. \tag{1a}$$

The first and second terms on the right-hand side of equation (1a) represent the reproduction of adult insects. The number of eggs in patch l increases with the number of reproductive-type adults in patch l and the number of dispersal-type adults immigrating from other patches. Dispersal-type adults have a mortality rate m during dispersal. The number of dispersal-type adults immigrating from other patches is greater when the resources available in the focal patch are higher compared with elsewhere. In equation (1a), the number is proportional to $R_l/\bar{R}$, where $\bar{R}$ is the average across all the patches. The third term of equation (1a) represents the growth of eggs to the first larval stage at a rate gR_l. The fourth term represents the death of eggs with mortality rate u.

The dynamics of the four larval stages ($i = 1, 2, 3, 4$) and of adults ($i = 5$) are given as follows:

For larvae in the sensitive stages (i.e. for $i = 1$–3):

larvae develop into reproductive-type adults:

$$\frac{dN_{i,l}^{0}}{dt} = gR_l N_{i-1,l}^{0} - gR_l N_{i,l}^{0} - h(B_l, R_l) - uN_{i,l}^{0}, \tag{1b}$$

or larvae develop into dispersal-type adults:

$$\frac{dN_{i,l}^{1}}{dt} = gR_l N_{i-1,l}^{1} - gR_l N_{i,l}^{1} + h(B_l, R_l) - uN_{i,\lambda}^{1}. \tag{1c}$$

For larvae in the non-sensitive stage ($i = 4$):

$$\frac{dN_{4,l}^{j}}{dt} = gR_l N_{3,l}^{j} - gR_l N_{4,l}^{j} - uN_{4,l}^{j}, \quad j = 0, 1. \tag{1d}$$

For adults ($i = 5$):

$$\frac{dN_{5,l}^{j}}{dt} = gR_l N_{4,l}^{j} - uN_{5,l}^{j}, \quad j = 0, 1. \tag{1e}$$

All larvae begin life as reproductive-type individuals, but some of them may transform into the dispersal type, yielding adults of both the dispersal type and the reproductive type.

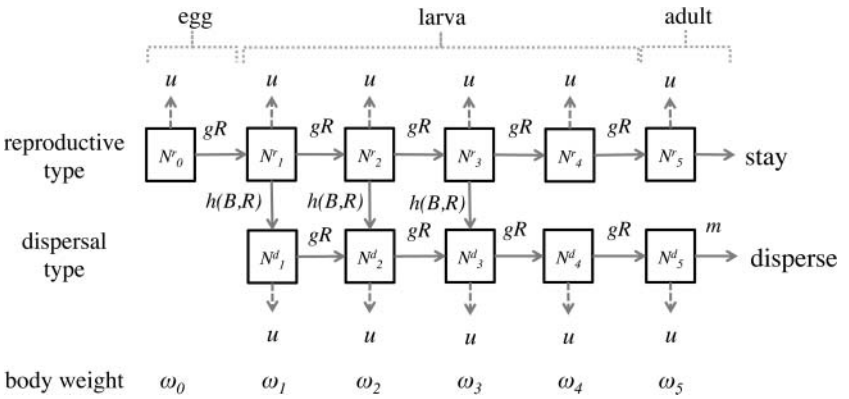

Fig. 1. Schematic representation of the life cycle of insects. Solid arrows indicate growth to the next developmental stage. Broken arrows indicate insects removed as a result of dying.

Transition rate

Larvae develop into the reproductive type under low-density conditions. The rate of transition to the dispersal type increases as density within the patch increases. Here we denote biomass by B_l, which is defined as

$$B_l = \sum_i \sum_j N_{i,l}^j \omega_i, \tag{2}$$

where ω_i is the body weight of larvae in the ith stage. Here, density in the patch is defined as the biomass per unit resource and is given by B_l/R_l. We assume that the rate of transition from the reproductive type to the dispersal type is a linear function of density in the patch:

$$h(B_l, R_l) = \begin{cases} \alpha \times (B_l/R_l) + \beta, & \text{if it is positive} \\ 0, & \text{otherwise} \end{cases}, \tag{3}$$

where α and β indicate the response of the insect to density in the patch. We treat both of these as quantitative traits that evolve by natural selection.

Larval growth rate

Larvae in stage l grow to the next stage $l + 1$ at a rate gR_l, where R_l is the resource abundance and g is the growth rate. Resource abundance R_l follows the dynamics given by

$$\frac{dR_l}{dt} = rR_l\left(1 - \frac{R_l}{K_l}\right) - gB_lR_l. \tag{4}$$

The first term on the right-hand side of equation (4) represents the rate of growth of resources, while the second term on the right-hand side represents consumption of resources by the insect larvae in the same patch at a rate proportional to their biomass B_l.

Environmental fluctuation

We assume that the carrying capacity of the resources fluctuates between high and low values periodically. The same environment lasts for time T. We regard the difference between these two values as the intensity of environmental fluctuation.

EVOLUTIONARY DYNAMICS

We traced the evolutionary change of two parameters (α and β) that control the rate of transition from the reproductive type to the dispersal type, which is given by equation (3). The evolutionary dynamics consists of the following steps:

1. *Simulating the resident population dynamics*. Initially, all patches contained only eggs of the resident type with both α and β equal to zero, producing reproductive-type individuals. Then the resident population was allowed to grow and disperse for a sufficiently long time.
2. *Introduction of a rare mutant*. Mutant individuals were introduced into all patches at a low frequency. In the numerical analyses in this paper, the initial proportion of mutants was 0.001, or 0.1% of the total population, which was common to all patches. The parameters of the mutant were distributed around those of the resident. Specifically, the traits of the mutant were those of the resident plus a normally distributed random variable with a mean of zero and standard deviation of 0.01.
3. *Invasibility of the mutant*. The population dynamics of the resident and the mutant were traced for a sufficiently long period. After the evolutionary simulation runs, if the proportion of mutants was greater than 0.1% of the population as a whole, we considered the mutant to be capable of invading a population dominated by the resident. In contrast, if the proportion of mutants was less than 0.1%, we considered the mutant to be incapable of invading the population.
4. *Simulation in the next round*. If the mutant succeeded in invading the population, we considered that it would out-compete the resident and replace it. In the next round of evolutionary simulation, the mutant became a resident and a new mutant was chosen at random following the rules outlined above. If the mutant failed to invade, we considered the resident to be successful in its defence against invasion, and it remained the resident in the subsequent round. Thus a new mutant was again chosen.

We repeated this procedure (i.e. generating a novel mutant and examining its success/failure to invade) for 1600 trials. Traits α and β converged to a pair of values. We regard these as the evolutionary endpoint.

RESULTS

Here we summarize the results of the evolutionary simulations, in particular the effect of each parameter on the propensity for evolution of density-dependent dispersal and on the magnitude of density dependence.

Magnitude of environmental fluctuation

We observed how the intensity of environmental fluctuation affects the evolution of α and β with regard to transition rate, $h(B_l, R_l)$. We set a fixed value of 15 for the high carrying capacity (K_h), and varied the value of the low carrying capacity (K_l) from 1 to 8. We defined the intensity of environmental fluctuation as K_l/K_h, the difference between the high and low carrying capacities. An example of the evolutionary trajectories of α and β is given in Fig. 2. We assumed that α and β converged to narrow ranges regardless of their initial values. We then calculated the average value of α and β over the final 100 rounds of evolutionary simulation. The results are shown in Fig. 3.

When there was high environmental fluctuation, α evolved to a positive value, whereas β at transition rate $h(B_l, R_l)$ evolved to a negative value. As the intensity of environmental fluctuation decreased, the evolutionary outcomes of α and β moved closer to zero, and finally they became zero.

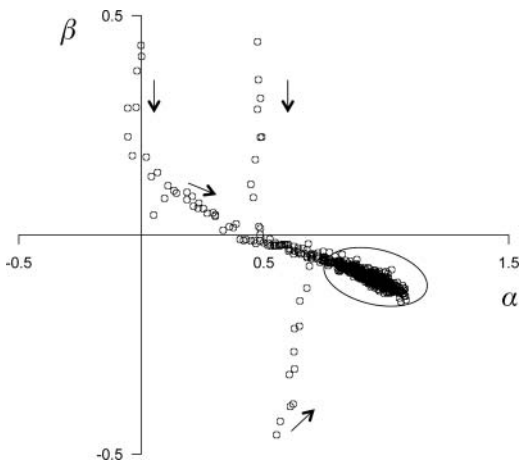

Fig. 2. The evolutionary trajectories of α and β starting from different initial conditions. The initial conditions were: (α, β) = (0.0, 0.0), (0.5, 0.0), (0.0, 0.5), (0.5, 0.5), (0.5, −0.5). Parameter values were: $r = 0.5$, $g = 0.1$, $u = 0.3$, $m = 0.05$, $f' = 1.5$, $f^d = 1.0$.

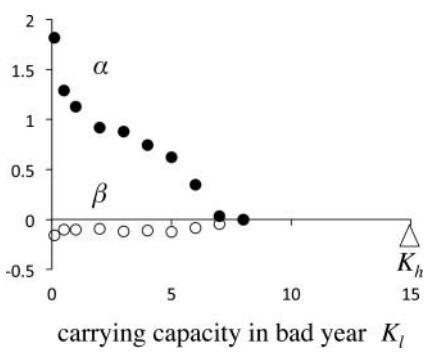

Fig. 3. Parameters α and β evolved under different intensities of environmental fluctuation. Solid circles (●) represent α values; open circles (○) represent β values. Parameter values are the same as in Fig. 2.

We also examined the dependence of the evolutionary outcomes of α and β on parameters affecting the resource dynamics and the growth of organisms in a patch, such as growth rate g, mortality u, recovery of resources r, and dispersal mortality m. We set $K_h = 15$ and $K_l = 2$ in the following simulations.

Growth rate

We observed the effect of growth rate g on the evolution of α and β (Fig. 4a). In Fig. 4a, the vertical axis shows the values of α and β in the simulations, while the horizontal axis indicates growth rate g. When g was small, the absolute values of α and β were large. When g was large, α and β were small. This result implies that when growth rate g was large, the production of dispersal-type individuals as a result of high density was suppressed.

Mortality during each of the developmental stages

We observed the effect of mortality u on the evolution of α and β (Fig. 4b). In Fig. 4b, the vertical axis indicates the values of α and β in the simulations, while the horizontal axis represents mortality u. When u was small, the absolute values of α and β were small. This result suggests that the production of dispersal-type individuals as a result of high density was curtailed with lower mortality.

Recovery of resources

Figure 4c shows the effect of the recovery of resources r on the evolution of α and β. The horizontal axis represents the rate of recovery of resources r. When the rate of recovery of resources was low, the absolute values of α and β were large; but when r was high, α and β were small (Fig. 4c). When the rate of recovery of resources was high, resource depletion due to larval feeding was low, and the production of dispersal-type individuals as a result of high density was low.

Dispersal mortality

Figures 4d and 4e illustrate the effect of dispersal mortality m on the evolution of α and β under different magnitudes of environmental fluctuation. In Figs. 4d and 4e, the vertical axis indicates values of α and β, and the horizontal axis represents dispersal mortality m. We set $K_h = 15$. When $K_l = 6$, the absolute values of α and β became smaller as dispersal mortality increased. This implies that a larger dispersal mortality m discouraged the production of dispersal-type individuals at high density. When environmental fluctuation was high ($K_l = 2$), α and β became larger as dispersal mortality increased. This implies that higher dispersal mortality enhances the production of dispersal-type individuals at high density, which is opposite to the effect seen with low environmental fluctuations ($K_l = 6$).

Period during which carrying capacity was maintained at a constant level

We assumed that the carrying capacity of each patch varies periodically. Figure 5a illustrates the effect of the length of environmental fluctuation on the evolution of α and β. The horizontal axis represents the periodicity of environmental fluctuation. When the

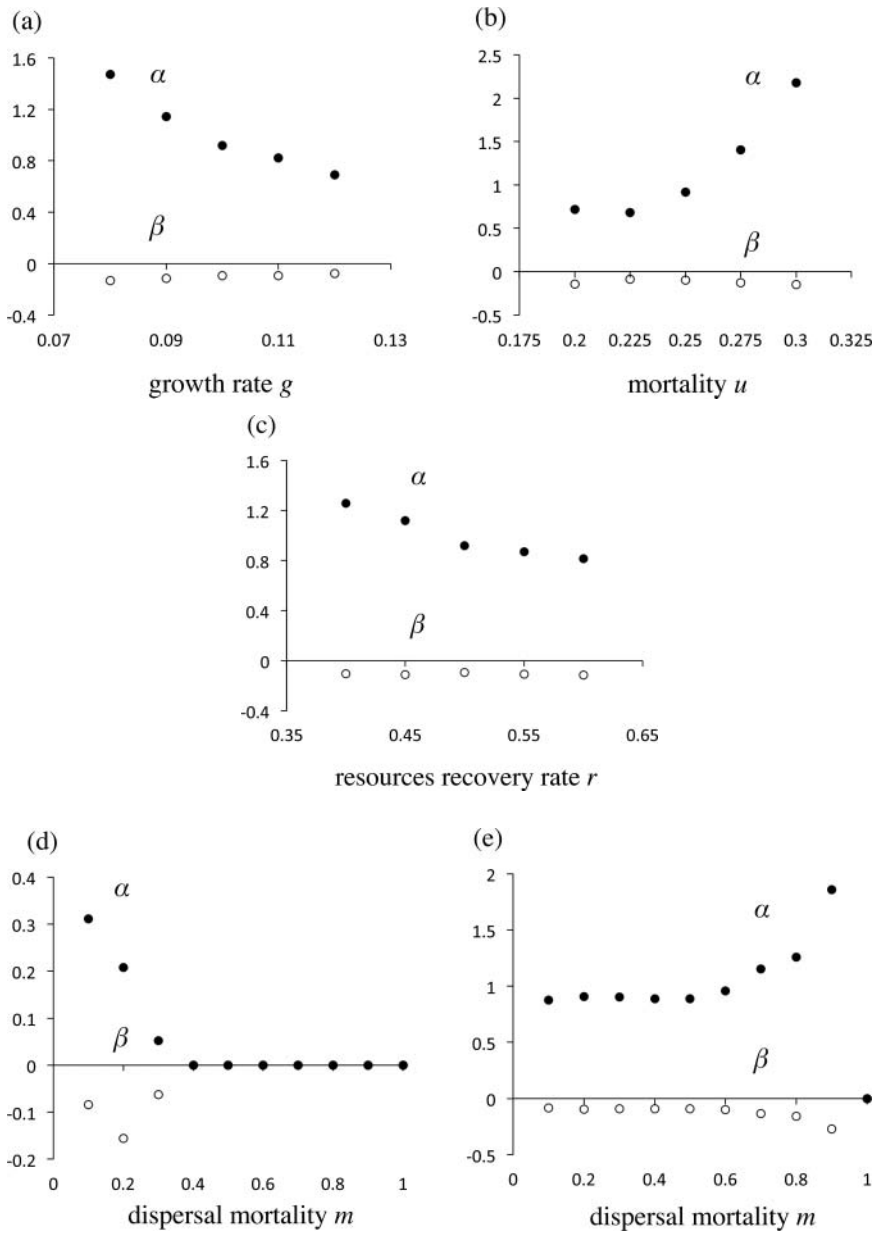

Fig. 4. Parameter dependence: (a) growth rate g, (b) mortality u, (c) rate of recovery of resources r, and (d–e) dispersal mortality m on the evolution of α and β. (d) $K_l/K_h = 0.13$, (e) $K_l/K_h = 0.4$. Solid circles (●) represent α values; open circles (○) represent β values. Parameter values are the same as in Fig. 2.

environmental fluctuation was short in duration, the absolute values of α and β were large. This implies that when the period of environmental fluctuations is long in duration, the production of dispersal-type individuals at high density decreases.

Carrying capacity level switches following a Markov chain

We studied the evolution of density-dependent dispersal when the fluctuation in carrying capacity was random based on the following rules (Fig. 5): when the carrying capacity in a patch is K_h, then over a short interval of length Δt, the carrying capacity becomes K_l with probability $p\Delta t$ or remains K_h with probability $1 - p\Delta t$. When the carrying capacity in a patch l is K_l, then over a short interval, the carrying capacity becomes K_h with probability $q\Delta t$ or remains K_l with probability $1 - q\Delta t$. Hence the duration over which the carrying capacity is maintained at a constant level follows an exponential probability distribution with mean $1/p$ and $1/q$, respectively.

As $p(=q)$ increased, the interval during which each environment remained the same decreased, and the absolute values of α and β became larger. This suggests that as changes to the environment become more frequent, a density-dependent dispersal rate is more likely to evolve.

Biomass per patch versus biomass per unit resource

So far, we have considered the type-transition rule based on the biomass per unit resource, as shown in equation (3). We now consider a different type-transition rule in which the transition rate increases with the biomass per patch:

$$h(B_l) = \begin{cases} \alpha' \times B_l + \beta', & \text{if it is positive} \\ 0, & \text{otherwise} \end{cases}, \tag{5}$$

where α' and β' are the variables that evolve. This we call the B-rule, in contrast to equation (3), which we call the B/R-rule. We wished to study the B/R-rule represented by equation (3)

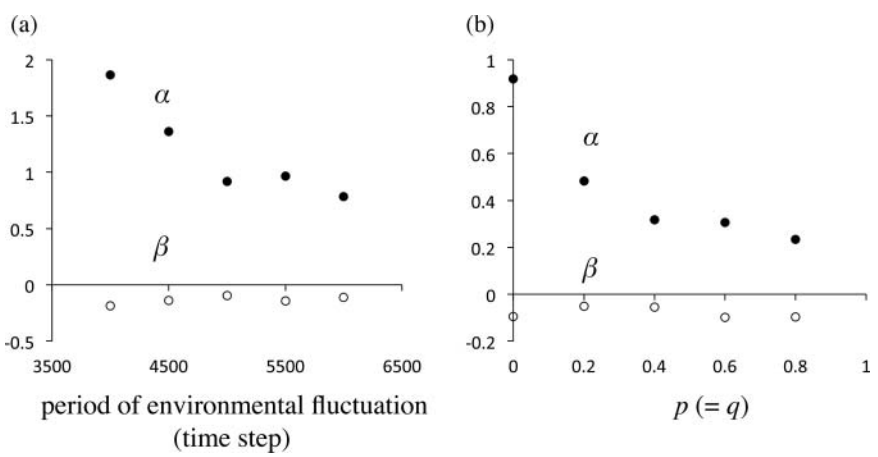

Fig. 5. Effect of temporal stability on the evolution of α and β. Solid circles (●) represent α values; open circles (○) represent β values. Parameter values are the same as in Fig. 2.

and the B-rule represented by equation (5) when in competition with each other. We first examined the evolution of the type indicated by equation (3), in which two parameters, α and β, evolve. We then examined the evolution of the type indicated by equation (5), where α' and β' evolve. Then we let these two types compete with each other and observed which outcompeted the other. We examined the invasibility of a rare type in a population dominated by the other type. For example, we examined whether a rare B-rule increases in a population dominated by the B/R-rule, and whether a rare B/R-rule increases in a population dominated by the B-rule. If the B-rule increases both when it is rare and when it is dominant, we can conclude that it outcompetes the B/R-rule. In contrast, if the B-rule decreases in both contexts, we can conclude that the B/R-rule outcompetes the B-rule. If, instead, the rare B-rule increases in a population dominated by the B/R-rule, and a rare B/R-rule increases in a population dominated by the B-rule, then we can conclude protected polymorphism, suggesting the co-existence of the two types in the population.

We let the two types compete 100 times for each set of parameters, and determined the winner. The results are shown in Fig. 6. When $K_l/K_h = 0.47$ or 0.40, the B-rule defeated the B/R-rule. When $K_l/K_h = 0.07$, 0.13, 0.27 or 0.33, the B/R-rule defeated the B-rule. When $K_l/K_h = 0.01$ or 0.03, the two rules were found to co-exist. We conclude that when environmental fluctuation is strong ($K_l/K_h \leq 0.33$), dispersal based on biomass relative to resource (B/R-rule) is more likely to evolve than dispersal based only on biomass. Interestingly, when environmental fluctuation is mild ($K_l/K_h \geq 0.4$ or more), dispersal based on biomass only (B-rule) is more likely to evolve than dispersal based on the ratio of biomass to resource abundance.

DISCUSSION

Our theoretical study predicts that dispersal rate increases with density ($\alpha > 0$, $\beta < 0$) and is more likely to evolve when environmental fluctuation is strong. All adults in a patch will become reproductive-type individuals at low density, but some dispersal-type adults will be produced if the density is above a certain threshold. This is consistent with previous theoretical studies on density-dependent dispersal that did not explicitly consider the dynamics of resources within each patch or the resource-dependent growth of the organisms (Ezoe and Iwasa, 1997; Travis *et al.*, 1999; Poethke and Hovestadt, 2002; Amarasekare, 2004; Kun and Scheuring, 2006; Hovestadt *et al.*, 2010; Rodrigues and Johnstone, 2014). It is also consistent with field observations in insects. For example, in wing-polymorphic insects, populations collected in highly fluctuating environments such as croplands tend to produce more macropterous individuals than do those in stable environments (Denno *et al.*, 1991; Zera and Denno, 1997). In wing-polymorphic insects, determination of wing type in response to density differs among populations (Iwanaga *et al.*, 1985, 1987). Furthermore, environmental fluctuation affects wing determination in response to density (Denno *et al.*, 1991).

Below we analyse the effects of different model parameters on the pattern of density-dependent wing determination.

Growth rate and mortality rate

In this study, we explicitly considered the stage structure of the population to consist of an egg stage, four larval stages, and a final adult stage. The production of dispersal-type adults was promoted by a slower growth rate (Fig. 4a). This prediction is supported by empirical

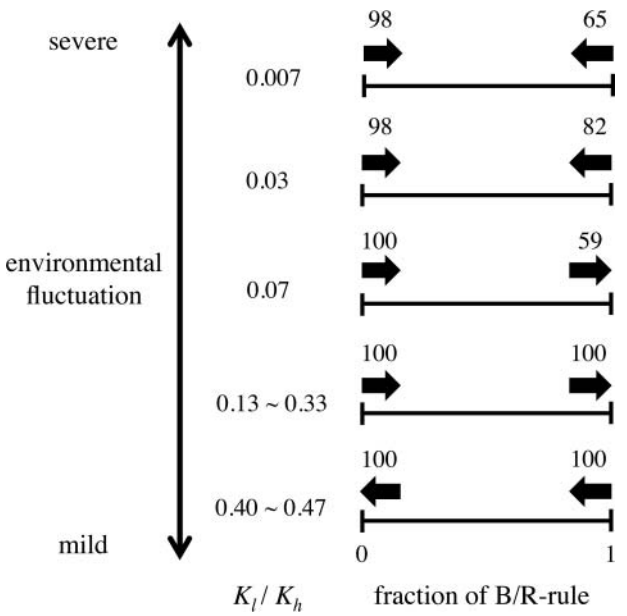

Fig. 6. Invasibility analysis of dispersal based on biomass relative to resource (B/R-rule) and dispersal based on biomass only (B-rule). Horizontal axes indicate the proportion of B/R-rule in the population. We examined the change in the proportion of the two types when the fraction of the B/R-rule was close to one (B/R-rule dominant) and when it was close to zero (B/R-rule rare). The solid arrow indicates the direction of evolution judged from 100 simulation runs. Right facing arrows indicate that the B/R-rule beat the B-rule, while left facing arrows indicate that the B-rule beat the B/R-rule. The number above each arrow indicates the proportion of runs in which the outcome was the same as the arrow direction, indicating the reliability of the change. When environmental fluctuation is mild ($K_l/K_h = 0.40$–0.47), the B-rule ought to evolve; when environmental fluctuation is strong ($K_l/K_h = 0.07$–0.33), the B/R-rule ought to evolve. For $K_l/K_h = 0.03$, 0.007, the two types can co-exist. Parameter values are the same as in Fig. 2.

research showing that the availability of nutrients to host plants affects wing determination in wing-polymorphic insects (Sutherland, 1969; Muller *et al.*, 2001). The production of the dispersal type was also promoted by high larval mortality (Fig. 4b). Such results have not been reported in previous theoretical studies.

Resource recovery rate

We incorporated resource dynamics within each patch in the model. The analysis predicted a close relationship between the resource recovery rate and wing determination. When the resource recovery rate r was rapid, the production of dispersal-type individuals at high density was lower, because remaining in the patch is expected to be favourable even if the current high density in the patch suggests a rapid consumption of resources. Our results suggest that a rapid resource recovery rate enhances temporal stability and discourages the evolution of dispersal-type individuals at high density. Rodrigues and Johnstone (2014) reported that temporal stability in a habitat discourages dispersal, but their model did not explicitly consider patch resource dynamics.

In the field, the rate of growth of plant resources varies with climate and soil fertility. Therefore, the dispersal strategy of organisms in nature will also be affected by these factors.

Temporal mode of environmental fluctuation

In the present study, temporal stability was defined as the time for which the carrying capacity remains the same. When the environment was temporally stable, the production of dispersal-type individuals at high density was low (Figs. 5a, b). Note that in the present study, a shift in the carrying capacity affected the population dynamics only indirectly, because the model incorporated resource dynamics. Our results are consistent with those of previous models which assumed that growth rate depends directly on environmental fluctuation.

Dispersal mortality

Dispersal is costly and accompanied by many risks, such as physical injury and dangerous predators. Previous studies on density-dependent dispersal assumed that dispersal is accompanied by enhanced mortality and that higher costs lower the dispersal rate (Travis *et al.*, 1999; Poethke and Hovestadt, 2002; Kun and Scheuring, 2006).

In the present study, the effect of dispersal mortality was enhanced by the intensity of environmental fluctuation. When environmental fluctuation was low, the production of dispersal-type individuals was discouraged by the cost of dispersal (Fig. 4d). Our results are consistent with those of previous theoretical studies. In contrast, when environmental fluctuation was high, the production of dispersal-type individuals was promoted by the increase in dispersal cost (Fig. 4e). This result differs from previous studies. To understand the relationship between environmental fluctuation and dispersal mortality, more detailed analyses are required.

Biomass per unit resource

The density in a patch provides useful information for predicting future environmental conditions (Clobert *et al.*, 2009). We asked which of density defined in terms of biomass in a patch (B-rule) and density defined as biomass per unit resource (B/R-rule) is the better cue for predicting outcome. In a competition between the two types (Fig. 6), we showed that when the intensity of environmental fluctuation was weak, the B-rule was favoured to predict the future environment, whereas the B/R-rule was favoured in a fluctuating environment. Furthermore, when the intensity of environmental fluctuation was very strong, co-existence of the two phenotypes was possible. Such results have not been reported in previous theoretical studies.

Experimental studies of the physiological mechanisms of wing polymorphism in insects have been conducted for many years. In many wing-polymorphic insects, including plant hoppers, aphids, and crickets, the juvenile hormone plays an important role in wing determination (Hardie, 1980, 1981; Iwanaga and Tojo, 1986; Zera and Denno, 1997; Ishikawa *et al.*, 2013). In plant hoppers, for example, wing determination is affected by the juvenile hormone titre during the larval sensitive period (Iwanaga and Tojo, 1986). Larvae develop into the reproductive type if the juvenile hormone titre is above a certain threshold but become the dispersal type if the titre is below that threshold. The sensitive period starts during the early second instar stage

and continues into the fourth instar (Bertuso *et al.*, 2002). Recent studies have revealed that the insulin signal pathway that regulates growth dependent on nutrients also affects wing determination (Xu *et al.*, 2015; Guo *et al.*, 2016). Incorporating these hormonal dynamics into the model and examining the evolutionary outcomes based on the timing and the magnitude of production and decomposition of the hormones would be a useful extension of the current study.

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