A MODELLING EXERCISE TO SHOW WHY POPULATION MODELS SHOULD INCORPORATE DISTINCT LIFE-HISTORIES OF DISPERSERS

Jacques A. Deere[1]*, Ilona van den Berg[2], Gregory Roth[1,3], Isabel M. Smallegange[1]

[1] Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94240, 1090 GE Amsterdam, The Netherlands

[2] Vrije Universiteit, Faculty of Earth and Life Sciences, Department of Animal Ecology, The Netherlands

[3] Friedrich Miescher Institute for Biomedical Research, Maulbeerstrasse 66, P.O. Box 3775, 4002 Basel, Switzerland

*Corresponding author address:
Institute for Biodiversity and Ecosystem Dynamics (IBED), University of Amsterdam, P.O. Box 94240, 1090 GE Amsterdam, The Netherlands

E-mail addresses:

Jacques A. Deere (corresponding author):	jacquesdeere@gmail.com
Ilona van den Berg:	ilonavdberg@hotmail.com
Gregory Roth:	gregory.roth@fmi.ch
Isabel M. Smallegange:	i.smallegange@uva.nl

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Abstract

Dispersal is an important form of movement influencing population dynamics, species distribution, and gene flow between populations. In population models, dispersal is often included in a simplified manner by removing a random proportion of the population. Many ecologists now argue that models should be formulated at the level of individuals instead of the population-level. To fully understand the effects of dispersal on natural systems, it is therefore necessary to incorporate individual-level differences in dispersal behaviour in population models. Here we parameterised an integral projection model (IPM), which allows for studying how individual life histories determine population-level processes, using bulb mites, *Rhizoglyphus robini*, to: (i) assess whether or not accounting for life-history differences between residents and dispersers affect natal population growth rates, and (ii) assess to what extent dispersal expression (frequency of individuals in the dispersal stage) and dispersal probability affect the proportion of dispersers and natal population growth rate. We find that ignoring life-history differences between residents and dispersers underestimates the population growth rate and overestimates the proportion of the population that disperse as dispersal probabilities increase. Furthermore, allowing for life-history differences between residents and dispersers shows that multiple combinations of dispersal probability and dispersal expression can produce the same proportion of leaving individuals. Additionally, a given proportion of dispersing individuals results in different natal population growth rates. The results highlight that dispersal life histories, and the frequency with which dispersers occur in the natal population, significantly affect population-level processes. Thus, biological realism of dispersal population models can be increased by incorporating the typically observed life-history differences between residents and dispersers, and we here present a methodology to do so.

Introduction

The movement of individuals is one of the key mechanisms shaping biodiversity (Travis and Dytham 1999; Jeltsch et al. 2013). An important form of movement is dispersal, which is any movement of individuals or propagules with potential for gene flow across space (Ronce 2007; Bonte et al. 2012). Dispersal influences the dynamics and persistence of populations, the distribution and abundance of species, the community structure, and the level of gene flow between populations (Brown and Kodric-Brown 1977; Dieckmann et al. 1999; Hanski 1999; Bowler and Benton 2005). In so doing, dispersal can fuel evolutionary processes such as local adaptation and speciation (Dieckmann et al. 1999). Currently, understanding dispersal behaviour is important to be able to predict how populations will respond to some of the most important threats to biodiversity, such as climate change, habitat loss and fragmentation, and the invasion of alien species (Bowler and Benton 2005; Clobert et al. 2009).

In the last decades, the drivers of dispersal have been the centre of many theoretical studies (Hamilton and May 1977; Johnson and Gaines 1990; Hanski 1999; Clobert et al. 2004). However, the dispersal process itself has gained less attention. Due to practical problems associated with the study of dispersal in the field, much of dispersal research has taken a theoretical approach (Bélichon et al. 1996; Bowler and Benton 2005). In population models, dispersal is often considered as a population-level process, in which a proportion of the population leaves (Clobert et al. 2004; Bowler and Benton 2005). In such models, individual-level differences are often ignored, which means that any individual within the population has the same probability of dispersing successfully. However, recently it has been argued that population ecology should shift its focus from formulating models at the population level to the level of individual organisms (Clark et al. 2011; Topping et al. 2015; Soudijn and Roos 2017); an argument echoed in the field of dispersal (Bonte et al. 2012). Although ecological

patterns can be observed at the population level, it is the behaviour and demographic changes of individuals that shape the dynamics of the population (Clark et al. 2011; Soudijn and Roos 2017). So, in order to fully understand the effects of dispersal on natural systems, it is necessary to incorporate individual-level differences in dispersal behaviour in population models.

Empirical studies have shown that dispersing individuals typically have different demographic properties compared with residents (individuals that remain in the population) (Harrison 1980; Bélichon et al. 1996; O'Riain et al. 1996; Lemel et al. 1997; Zera and Denno 1997; Deere et al. 2015). Dispersers and residents can differ in their morphology, physiology or in their behaviour (Bélichon et al. 1996; Clobert et al. 2009; Bonte et al. 2012). In many species, an individual property, e.g. locomotory movement, which potentially serves many important functions, is enhanced for dispersal (Phillips et al. 2006; Bonte et al. 2012). In other species, dispersers develop a morphology primarily as an adaptation for dispersal, e.g. the development of wings or structures which facilitate attachment to mobile vectors (Harrison 1980; Zera and Denno 1997; Diaz et al. 2000; Bonte et al. 2012). Species with a distinct disperser morphology are ideal study systems to investigate the individual-level effects and adaptive significance of dispersal in natural populations. For many of these species, each genotype has the potential to develop into a disperser or a resident (Harrison 1980; Clobert et al. 2004). The investment in a disperser morphology is costly if it requires resource investment, likely at the expense of investment into body condition or fecundity (Lemel et al. 1997; Bonte et al. 2012; Deere et al. 2015). Such investment costs, defined as "pre-departure costs", arise during development prior to the actual dispersal event, although they may be deferred to later in the life-history as well (Bonte et al. 2012). However, not all individuals that invest in dispersal morphology leave their natal population, e.g. due to a behaviour or

physiological component affecting dispersal propensity (Roff and Fairbairn, 2001), reduced patch accessibility (Clobert et al. 2001) or environmental conditions (Johnson 1969). In order to make the dispersal process in population models more realistic and its results more biologically relevant, an individual-based method that takes distinct dispersal life-histories and (un)successful dispersal into account is necessary. Here, we do so using an approach that incorporates these distinct dispersal life-histories into a population model structured by life stage. The output of the model is then compared to that of a model that does not account for distinct dispersal life-histories to unravel how dispersal characteristics affect natal population dynamics. Finally, the effect of dispersal in the more complex model can be analysed. As a first step towards such an approach we apply the model to the bulb mite (*Rhizoglyphus robini*, Claparède).

The bulb mite is an ideal model system to study dispersal as it has a distinct dispersal stage within its life-history. We model the system using Integral Projection Models (IPMs) as they comprise individual-level functions that describe demographic rates (thereby tracking fluctuations in population size and structure), they can be applied to species with complex demography, require relatively straightforward mathematical techniques from matrix calculus, and are closely and easily linked to field and experimental data (Easterling et al. 2000; Ellner and Rees 2006). We parameterise two IPMs to test our approach, and in both dispersal occurs in a juvenile stage. In the first model, henceforth Distinct Disperser Phenotype Model (DDPM), we incorporate a distinct dispersal life-history where a dispersal stage is included in the life-cycle. Each individual has the potential to develop into a disperser (i.e. develop into the dispersal stage) or a resident (i.e. do not develop into a disperser stage), and each disperser has the option to leave the natal population (“successful disperser”) or remain in the natal population (“unsuccessful disperser”) (Fig. 1). The natal population will thus consist

of residents and unsuccessful dispersers (given the proportion of “successful dispersers”). It is important to note that unsuccessful dispersers in the context of this study refers to disperser individuals that do not emigrate from the population; not to disperser individuals that do not survive the transfer phase or fail to establish in a new habitat. The second model ignores a distinct dispersal life-history, henceforth Naïve Model (NM); when dispersal occurs, it occurs in the final juvenile stage. As such, within the model, the life-histories of dispersing individuals are similar in their life-histories to residents in terms of the number of juvenile development stages and in terms of dispersal ability of individuals within the juvenile stage that dispersers (unlike the DDPM, all individuals in the final juvenile stage can disperse) (see Fig. 2). Prior research has shown that the presence of unsuccessful dispersers in the natal population has population-level consequences; population growth rate and mean lifetime reproductive success decrease and generation time increases with increasing proportions of unsuccessful dispersers (Deere et al. 2017). However, the work by Deere et al. (2017) did not incorporate emigration from the natal population, and thus did not show whether the effects they found would also hold when including emigration from the natal population. Here we build upon this work, but, to address our aim of understanding how distinct dispersal life histories play a role in natal population-level processes during a dispersal event, we define two objectives. First, to compare the effects of dispersal probability (probability that dispersing individuals emigrate) in a model where dispersers and residents have distinct life-histories (Distinct Disperser Phenotype Model) versus a model where all individuals have the same life-histories (Naïve Model) on the structure (in terms of proportion of dispersers that ultimately emigrate) and growth rate of the natal population. Second, in the Distinct Disperser Phenotype Model, quantify the effects of the expression of a distinct disperser phenotype (frequency of

individuals developing into dispersers) and dispersal probability on the proportion of dispersers and growth rate of the natal population (Fig. 1).

Methods

Study system and life-history data

Bulb mites consist of five life stages but develop a dispersal stage (called the deutonymph stage) under unfavourable environmental conditions (e.g. low temperature, humidity, food quality) (Diaz et al. 2000) (Fig. 2). The dispersal stage is non-feeding and occurs in both sexes. We use the same life-history data on female bulb mites as used in Deere et al. (2017) to parameterise the IPMs; these data provide information on individuals that do and do not develop into the deutonymph stage as life histories differ between individuals that went through the deutonymph stage and those that did not (for detailed data collection see Deere et al. (2015), data can be found in the figshare repository 10.6084/m9.figshare.1312875).

Distinct Disperser Phenotype Model (DDPM)

The DDPM has a distinct dispersal stage, the deutonymph stage, which allows for emigration. Dispersal is a two-step process that consists of development into a disperser (deutonymph) and dispersal out of the population (Fig. 3). Deutonymph expression, β, describes the transition probability of developing from a protonymph to a deutonymph. Dispersal probability, δ, describes the probability of a deutonymph leaving the population (Fig. 3). Note that both rates are size independent in this system (Deere et al. 2017), but size dependence can easily be incorporated.

To build the DDPM, we extend the size- and stage- structured IPMs developed by Deere et al. (2017) by including an emigration component. An IPM tracks fluctuations in population size and structure based on individual-level processes. The IPM projects a new stage-size joint distribution based on the stage-size joint distribution in the previous time step (Easterling et al. 2000; Coulson 2012; Deere et al. 2017). In each time step, individuals may survive, disperse, grow and produce new individuals. These processes are captured in a kernel that describes how the body size *z*, and stage *s*, joint distribution at time *t*, $n_t(z,s)$, is influenced by survival, dispersal, growth, reproduction and the parent-offspring association (the size of offspring, *z'*, produced by females of a certain size, *z*, at time *t*), resulting in a new joint distribution at time *t*+1:

$$n_{t+1}(z',s') = \sum_{s=1}^{8} \int_{\Omega} K(z',s',z,s) n_t(z,s) dz \qquad (1)$$

where Ω designates the range of individual sizes. The IPM kernel, K, is composed of two parts,

$$K = S(z,s)D(z,s)T(s',z,s)G(z',z,s) + R(z,s)O(z',z,s) \qquad (2)$$

The first part describes how individuals grow, survive and move: S(*z*,*s*) is the survival probability to the next time step of an individual in size *z* and stage *s*; D(*z*,*s*) is the probability that an individual of size *z* in stage *s* stays in the population in the next time step; T(*s'*,*z*,*s*) is the probability that an individual in size *z* and stage *s* develops into the new stage *s'* and G(*z'*,*z*,*s*) is the probability that an individual in size *z* and stage *s* growths to size *z'*. The second part describes adult reproduction: R(*z*,*s*) is the number of offspring produced by an adult individual of size *z* in stage *s* and O(*z'*,*z*,*s*) is the probability that offspring produced by adults of size *z* is of size *z'*. IPM equations (Table A1 equations 3.1 to 3.12), and parameter values used, can be found in the appendix.

The order of the functions in the kernel K represents the sequence of events in each time step, and the point at which the population is censused. This order is crucial for the outcome of the IPM (Rees et al. 2014). The order of events in this IPM is first survival, then dispersal, then transition and lastly growth. Dispersal is applied prior to transition in order to track all individuals that develop into the deutonymph stage (the dispersing individuals). Since dispersal is only possible for individuals in the deutonymph stage (i.e. dispersal stage), the probability to stay in the population is equal to 1 for all individuals in all stages other than the deutonymph stage. For all individuals in the deutonymph stage, the probability to stay in the population is $1 - \delta$ which is independent of its size.

Naïve Model (NM)

The construction of the NM is the same as that for the DDPM. The NM differs to the DDPM in that it lacks the distinct dispersal stage but allows for emigration to occur from another juvenile stage; the tritonymph stage. Therefore, in the NM, the dispersal process only consists of emigration of juvenile individuals in the final juvenile stage (Fig. 3) and does not include transitioning into a distinct dispersal phenotype. Individuals in the tritonymph stage leave the population with a probability γ. The IPM equations for the NM can be found in Table A1 of the appendix (equations 4.1 to 4.5). The dispersal function D in the NM was calculated using dispersal probability γ applied to tritonymphs, contrary to the dispersal function D in the DDPM which used δ and applied to deutonymphs (Fig. 3).

Models parameterization and analysis

Models were parameterised from life-history data of female bulb mites (see *Study system and life-history data*). In the case of the DDPM, the distinct dispersal stage was

parameterised from individuals that developed into the dispersal stage (the deutonymph). In the case of the NM, these individuals were still included in the data for parameterisation but were combined with the protonymph stage (stage preceding the tritonymph stage) (Fig. 3). The idea behind combining these two life stages stems from the fact that, by including dispersing individuals when estimating parameters of the vital rates for the NM, any individual costs of these individuals will be incorporated into these rates and will be reflected to some extent in the population. This would be indicative of empirical data where, within a population, dispersing individuals were not identified but were present and sampled.

Once parameterised, each function is then discretised into a matrix form by dividing the full size domain into very small-width discrete bins ('mesh points'; see appendix for details). These discretised matrices describe the predicted transition rates and are used to build a projection matrix that approximates the IPM, so standard methods for analysing matrix population models can be used (Caswell 2001; Coulson 2012). Details on how the functions were parameterized can be found in the appendix. All analyses and simulations were performed in R version 3.0.2 (R Development Core Team 2013).

Model comparisons

We compare a model that describes the distinct dispersal stage (DDPM) to a model that does not (NM). To be able to compare these two models, they both have to represent the same population, and therefore we fit them to the same population. Hence, even though the NM represents a scenario where disperser individuals are not allocated a distinct dispersal phenotype, the costs of the dispersing individuals (e.g. reduced size, reduced reproductive output, increased development time; Deere et al. 2015) are still incorporated into the functions. While the value of β is calculated from the life-history data, we do not have data

for δ and γ. Therefore, we let δ vary between 0 and 1 and calculate the corresponding value of γ. That is, for a fixed value of δ, the value of γ was calculated in such a way that the proportion of individuals that disperse are the same in both models. The proportion of individuals that disperse in the DDPM (resp. NM) was calculated by integrating the stable stage distribution over the range of all sizes in the deutonymph stage (resp. tritonymph) and multiplying it with the dispersal probability δ (resp. γ). The stable stage distribution was calculated as the dominant right eigenvector of the projection matrix associated with each IPM (Easterling et al. 2000). Finally, the population growth rate, λ_0, was calculated as the dominant eigenvalue of the projection matrix associated to each IPM (Easterling et al. 2000).

Combination of disperser expression and dispersal probability

In the case of the DDPM we wanted to assess how an increase in disperser expression (β) and dispersal probability (δ) would affect population-level processes. Within the DDPM, β and δ were increased from 0-1 (at 0.01 increments) and for every combination of β and δ the proportion of individuals that disperse and λ_0 were calculated.

Results

Model comparisons

Comparing the outcomes of the two models, we found that population growth rates (λ_0) given by the DDPM and the NM are equal for only one value of δ (δ^* = 0.48) (Fig. 4A). For values smaller than δ^*, the NM underestimates λ_0, and for values greater than δ^*, the NM overestimates λ_0 compared to the DDPM. As δ increases the population growth rate given by the NM stays almost constant, while it decreases in the DDPM. Therefore, the difference between the maximum and minimum λ_0 values was higher for the DDPM (max = 1.26, min =

1.17) compared to the NM (max = 1.205, min = 1.198) (Fig. 4A). This is due to the fact that the low value of β produces only low proportions of dispersers in the DDPM while varying δ (black line, Fig. 4B). As a consequence, the equivalent range of values of γ in the NM that give those same proportion of dispersers is very narrow and close to 0 (red line, grey box bottom left Fig. 4B). The difference between the two growth rates of the two models is maximal for δ = 0.01 (difference = 0.055).

Combination of disperser expression and dispersal probability

When varying β and δ in the DDPM there is a non-linear, joint effect of dispersal expression and dispersal probability on the proportion of dispersing individuals (Fig. 5) and population growth rate (λ_0) (Fig. 6). If both β and δ increase then, in general, the proportion of dispersing individuals increases and λ_0 decreases. Reciprocally, if both β and δ decrease then, in general, the proportion of dispersing individuals decreases and λ_0 increases. When the changes in β and δ are opposed, any scenario (increase/decrease) in the proportion of dispersing individuals and λ_0 can occur (Table 1).

The joint effect of β and δ on the proportion of dispersers and λ_0 is not proportional. As a consequence, for a fixed proportion of dispersing individuals, multiple λ_0 values can occur (proportion of dispersing individuals: 0.04 (yellow line), 0.08 (red line), 0.12 (blue line); Fig. 5 & 6). Furthermore, with increasing proportions of dispersing individuals (blue line > red line > yellow line), the values of λ_0 encompassed by each proportion of dispersing individuals, decreases (Fig. 6). Another consequence of the joint effect of β and δ is unexpected scenarios in the proportion of dispersing individuals and λ_0 (grey dots in Table 1). For example, if β increases and δ decreases (in some specific proportion), then both the proportion of

dispersing individuals and λ_0 can decrease. Vice versa, if β decreases and δ increases (in some specific proportion), then both the proportion of dispersing individuals and λ_0 can increase.

Discussion

The need to incorporate complexity and realism in modelling dispersal (Bonte et al. 2012; Travis et al. 2012; Travis et al. 2013) has prompted a move to incorporate more individual heterogeneity and individual-level costs when modelling dispersal (Bonte et al. 2012). Here we incorporated individual heterogeneity, in terms of distinct life-histories for dispersing and non-dispersing individuals, as well as the individual-level cost of developing into a dispersing stage into population models. We first compare this model with a simpler model that does not account for distinct life-histories for dispersing and non-dispersing individuals, and then we assess the effects of these distinct life-histories on population-level processes.

Model comparisons

When modelling dispersal, dispersal rates are often applied to the whole population and the potential effect of dispersal to the natal population is then in terms of the proportion of the individuals that leave. We show that a model (NM), where dispersal probability is applied to all individuals within a life-stage, ultimately over- or under-estimates population-level parameters when compared to a model that accounts for distinct life-histories for dispersing and non-dispersing individuals (DDM). The population growth rate of the DDM decreases when the dispersal probability, δ, increases. However, the population growth rate of the corresponding NM is almost constant with a value between the maximum and the minimum population growth rate of the DDM. Therefore, the NM may under-estimate the

population growth rate ($\delta < \delta^*$) or over-estimate it ($\delta > \delta^*$), depending on the level of dispersal. The population growth rate of the NM is almost constant because the dispersal probability γ, as a function of the dispersal probability δ, is almost constant. This is a direct consequence of the very low value of β (estimated from the data) that implies a very low proportion of dispersing individual in the DDM (Fig. 4B) for all possible values of the dispersal probability δ. Indeed, in the DDPM, dispersal probability is applied only to individuals that develop into dispersing individuals, the dispersing stage (Fig. 3), and the deutonymph frequency is very low (β = 0.03). This means that very few individuals develop into dispersing individuals resulting in a lower proportion of dispersers and so the dispersal probabilities, regardless of how high they are, are only applied to a small proportion of the population. Therefore, very high dispersal probabilities would not reduce the proportion of adults in the population to such an extent that population growth rate will drop below one (Fig. 4A). These results highlight the fact that models that apply dispersal rates to all the individuals, and not specifically to dispersing individuals, may over- or underestimate quantities, like the population growth rate, that describe population dynamics.

Local population dynamics and dispersal rates between populations determines the ecological dynamics of metapopulations. Indeed, dispersal rate has a large effect on metapopulation dynamics and has shown to be influential in the propensity for dispersal-induced stability and synchrony within metapopulation models (Abbott 2011) and patch-level asymmetry (Benard and McCauley 2008). Our results are limited to a natal population perspective, however this may ultimately effect metapopulation dynamics. A study by Altermatt and Ebert (2010) has shown that, when considering the origin and number of migrants, metapopulation functioning may differ to the patterns of the generally considered view of colonization-extinction dynamics of metapopulations (e.g. Hanski and Gaggiotti 2004).

Altermatt and Ebert (2010) show that migrating stages occur in small and ephemeral habitat patches, contrary to colonization-extinction dynamics, and that these populations drive the metapopulation dynamics. In essence, they suggest that the focus should also be on where migrants colonizing a new habitat come from and in what numbers. Therefore, there is a need to accurately predict the proportion of dispersers that disperse from specific populations. We would further argue that the state of the natal population, given the presence of dispersing individuals (e.g. population growth rate; see Deere et al. (2017)), would then also become important in the context of a metapopulation. Furthermore, models inform conservation management decisions. Many metapopulation models are used to make predictions that drive conservation management decisions and potentially highlight areas of data paucity (Hanski 1999; Clobert et al. 2001; Calabrese and Fagan 2004; Peterson and Freeman 2016; Morin et al. 2017). Modelling the dynamics of populations is by its very nature a simplified version of reality. However, as more complexity is added to models in a manner that improves the biological realism of how dispersal rates are implemented, then not only can model performance be improved in terms of their realism, but also in terms of the accuracy of their predictions, which ultimately is more informative when used in management decisions (Clobert et al. 2001; Peterson and Freeman 2016).

Combination of disperser expression and dispersal probability

Given that the proportion of individuals that leave the population during a dispersal event is partly dependent on the number of disperser individuals within the population, we wanted to investigate the effect on the population of jointly manipulating the proportion of the dispersers in the population (β) and the dispersal probability (δ). Although we found a general trend for proportion of dispersers to increase (or decrease) and population growth

rate to decrease (or increase) when both dispersal parameters increase (or decrease), when the two parameters increase or decrease in *opposite* directions, a number of different outcomes of the population parameters can occur (Table 1). The outcomes include scenarios which one would largely expect; an increase in the proportion of dispersers and a decrease in population growth (or vice versa). For example, when the proportion of dispersers increase, population growth rate will decrease as these individuals leave the population and so do not contribute to the population growth. However, there are also outcomes that we did not expect; scenarios where both the proportion of dispersers and population growth rate decrease or increase together. The scenario where the proportion of dispersers and population growth rate decrease, occurs when β increases and δ decreases. An increase in the expression of deutonymphs results in more disperser individuals within the population, however, with lower dispersal probabilities, this would mean a reduced proportion of dispersers that emigrate. With fewer dispersing individuals leaving the population, the individual-level costs of investing in dispersal (i.e. reduced size at maturity, reduced lifetime egg production, increased development time) are then borne out at the population level, thereby reducing population growth rate (Deere et al. 2017). The scenario where both the proportion of dispersers and population growth rate increase, occurs when β decreases and δ increases. Here, reducing β reduces the expression of deutonymphs within the population, whereas increasing δ results in a larger proportion of the dispersing individuals leaving the population (i.e. an increase the proportion of dispersers). Population growth rate will increase as fewer dispersing individuals, with their associated individual-level costs of investing in dispersal, are left in the population and have a reduced effect on population growth rate. In all scenarios, expected and unexpected, the response is largely dependent on the ratio of the two dispersal parameters, highlighting that the population parameters are very responsive to

the joint effect of the two dispersal parameters. This outcome highlights that to fully understand the influence of dispersing individuals on natal population processes requires a detailed understanding of disperser life-histories and how the cost of investing in a disperser strategy is borne out at the population level, and to what extent dispersing individuals are present in the population.

Another key finding is that different population structures (multiple combinations of β and δ) can give the same proportion of disperser individuals (Fig. 5); this is significant because population structure can have a large effect on population growth. Previously, we have shown that, in the absence of emigration, distinct dispersal phenotypes within the natal population have different life-histories to non-dispersers and so do not contribute to population processes in the same way (Deere et al. 2017). Additionally, juveniles and adults do not always respond the same way to changing environmental and population conditions and so differ in their contribution to populations dynamics (Coulson et al. 2001; Ozgul et al. 2012). Furthermore, the influence that the frequency of dispersing individuals within the natal population and dispersal probability has on the proportion of dispersers can be seen as a natal-habitat induced effect. In this case the effects of the natal habitat on disperser phenotypes is clear, the expression of dispersing individuals is dependent on the quality of the natal habitat; however in other instances the effects may often be more subtle (e.g. maternal effects) (Benard and McCauley 2008). This effect on the proportion of dispersers can then further influence other processes such as genetic differentiation between populations (i.e. altering magnitude and/or symmetry of gene flow) (Benard and McCauley 2008). Indeed, Benard & McCauley (2008) highlight that environmentally induced asymmetries in the number or quality of dispersing individuals can lead to asymmetry in patterns of local adaptation. While our models are largely comparable to phoretic species, our findings are also

relevant to actively dispersing species. In species showing active dispersal, dispersal is often dictated by a combination of dispersal ability (e.g. structural formation such as wings) and dispersal propensity (e.g. behaviour or physiological component), which would influence the proportion of dispersers. Moreover, it has been suggested that interactions between these traits can generate non-linear relationships between habitat condition and net dispersal rates (Benard and McCauley 2008). All in all, it is the combination of natal-habitat induced effects on dispersal phenotypes and the population structure that will determine the proportion of dispersing individuals.

The importance of the joint effect of dispersal probability and the frequency of dispersing individuals within the population that we show, indicates the potential importance of accounting for the frequency of dispersing individuals within a population. We appreciate that our focus is on a specific study system, and do not suggest that our models are general in terms of their outcome. Rather we illustrate that the effects of dispersing individuals on natal populations are more than just a turnover of numbers. Given the importance of dispersal rates in (meta)populations, and that natural dispersal rates are being altered by human activities, how they are applied to populations then becomes vital. Only by identifying and including the individual-level costs dispersing individuals in a population, and applying dispersal rates to those individuals, can the full extent of the effects of dispersal to natal populations, and potentially metapopulations, start to be realised.

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Conflict of Interest

None

Author Contributions

JAD and IvdB conceptualized the study. JAD, IvdB and GR developed the models with input from IMS. JAD, IvdB, GR and IMS wrote and commented on the manuscript.

Data Accessibility

Dataset used for model parametrisation can be found in the figshare repository 10.6084/m9.figshare.1312875.

References

Abbott, K. C. 2011. A dispersal-induced paradox: synchrony and stability in stochastic metapopulations. Ecology Letters 14:1158–1169.

Altermatt, F., and D. Ebert. 2010. Populations in small, ephemeral habitat patches may drive dynamics in a Daphnia magna metapopulation. Ecology 91:2975–2982.

Bélichon, S., J. Clobert, and M. Massot. 1996. Are there differences in fitness components between philopatric and dispersing individuals? Acta Oecologia 17:503–517.

Benard, M. F., and S. J. McCauley. 2008. Integrating across Life-History Stages: Consequences of Natal Habitat Effects on Dispersal. The American Naturalist 171:553–567.

Bonte, D., H. Van Dyck, J. M. Bullock, A. Coulon, M. Delgado, M. Gibbs, V. Lehouck, et al. 2012. Costs of dispersal. Biological Reviews 87:290–312.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80:205–225.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. Ecology 58:445–449.

Calabrese, J. M., and W. F. Fagan. 2004. A comparison-shopper's guide to connectivity metrics. Frontiers in Ecology and the Environment 2:529-536.

Caswell, H. 2001. Matrix population models: Construction, analysis, and interpretation (Second.). Sinauer Associates, Sunderland, Massachusetts.

Clark, J. S., D. M. Bell, M. H. Hersh, M. C. Kwit, E. Moran, C. Salk, A. Stine, et al. 2011. Individual-scale variation, species-scale differences: inference needed to understand diversity. Ecology Letters 14:1273–1287.

Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols, eds. 2001. Dispersal. Oxford University Press, New York.

Clobert, J., R. A. Ims, and F. Rousset. 2004. Causes, mechanisms and consequences of dispersal. Pages 307–335 *in* I. Hanski and O. E. Gaggiotti, eds. Ecology, Genetics and Evolution of Metapopulations. Elsevier Academic Press Inc, Amsterdam.

Clobert, J., J. F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Coulson, T. 2012. Integral projections models, their construction and use in posing hypotheses in ecology. Oikos 121:1337–1350.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, et al. 2001. Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep. Science, New Series 292:1528–1531.

Deere, J. A., T. Coulson, S. Cubaynes, and I. M. Smallegange. 2017. Unsuccessful dispersal affects life history characteristics of natal populations: The role of dispersal related variation in vital rates. Ecological Modelling 366:37–47.

Deere, J. A., T. Coulson, and I. M. Smallegange. 2015. Life History Consequences of the Facultative Expression of a Dispersal Life Stage in the Phoretic Bulb Mite (Rhizoglyphus robini). PLoS ONE 10:e0136872.

Diaz, A., K. Okabe, C. J. Eckenrode, M. G. Villani, and B. M. Oconnor. 2000. Biology, ecology, and management of the bulb mites of the genus Rhizoglyphus (Acari : Acaridae). Experimental & Applied Acarology 24:85–113.

Dieckmann, U., B. O'Hara, and W. Weisser. 1999. The evolutionary ecology of dispersal. Trends Ecol Evol 14.

Easterling, M. R., S. P. Ellner, and P. M. Dixon. 2000. Size-specific sensitivity: Applying a new structured population model. Ecology 81:694–708.

Ellner, S. P., and M. Rees. 2006. Integral Projection Models for Species with Complex Demography. The American Naturalist 167:410–428.

Hamilton, W. D., and R. M. May. 1977. Dispersal in stable habitats. Nature 269:578–581.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, New York.

Hanski, I., and O. E. Gaggiotti, eds. 2004. Ecology, Genetics and Evolution of Metapopulations. Elsevier Academic Press Inc, Amsterdam.

Harrison, R. G. 1980. Dispersal Polymorphisms in Insects. Annual Review of Ecology and Systematics 11:95–118.

Jeltsch, F., D. Bonte, G. Pe'er, B. Reineking, P. Leimgruber, N. Balkenhol, B. Schroder, et al. 2013. Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. Movement Ecology 1:6.

Johnson, C. G. 1969. Insect migration and dispersal by flight. Methuen, London.

Johnson, M. L., and M. S. Gaines. 1990. Evolution of Dispersal: Theoretical Models and Empirical Tests Using Birds and Mammals. Annual Review of Ecology and Systematics 21:449–480.

Lemel, J.-Y., S. Belichon, J. Clobert, and M. E. Hochberg. 1997. The evolution of dispersal in a two-patch system: some consequences of differences between migrants and residents. Evolutionary Ecology 11:613–629.

Morin, D. J., A. K. Fuller, A. Royle, and C. Sutherland. 2017. Model-based estimators of density and connectivity to inform conservation of spatially structured populations. Ecosphere 8:e01623.

O'Riain, M. J., J. U. M. Jarvis, and C. G. Faulkes. 1996. A dispersive morph in the naked mole-rat. Nature 380:619.

Ozgul, A., T. Coulson, A. Reynolds, T. C. Cameron, and T. G. Benton. 2012. Population Responses to Perturbations: The Importance of Trait-Based Analysis Illustrated through a Microcosm Experiment. American Naturalist 179:582–594.

Peterson, J. T., and M. C. Freeman. 2016. Integrating modelling, monitoring, and management to reduce critical uncertainties in water resource decision making. Journal of Environmental Management 183:361-370.

Phillips, B. L., G. P. Brown, J. K. Webb, and R. Shine. 2006. Invasion and the evolution of speed in toads. Nature 439.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Rees, M., D. Z. Childs, and S. P. Ellner. 2014. Building integral projection models: a user's guide. Journal of Animal Ecology 83:528–545.

Roff, D.A., Fairbairn, D.J., 2001. The genetic basis of dispersal and migration, and its consequences for the evolution of correlated traits. In: Clobert, J., Danchin, E.,Dhondt, A.A., Nichols, J.D. (Eds.), Dispersal. Oxford University Press Inc., NewYork, pp. 191–202.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annual Review of Ecology Evolution and Systematics 38:231–253.

Soudijn, F. H., and A. M. Roos. 2017. Approximation of a physiologically structured population model with seasonal reproduction by a stage-structured biomass model. Theoretical Ecology 10:73-90.

Topping, C. J., H. F. Alrøe, K. N. Farrell, and V. Grimm. 2015. Per Aspera ad Astra: Through Complex Population Modeling to Predictive Theory. The American Naturalist 186:669–674.

Travis, J. M. J., M. Delgado, G. Bocedi, M. Baguette, K. Barton, D. Bonte, I. Boulangeat, et al. 2013. Dispersal and species' responses to climate change. Oikos 122:1532–1540.

Travis, J. M. J., and C. Dytham. 1999. Habitat persistence, habitat availability and the evolution of dispersal. Proceedings of the Royal Society of London B: Biological Sciences 266:723–728.

Travis, J. M. J., K. Mustin, K. a. Bartoń, T. G. Benton, J. Clobert, M. M. Delgado, C. Dytham, et al. 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods in Ecology and Evolution 3:628–641.

Zera, A. J., and R. F. Denno. 1997. Physiology and ecology of dispersal polymorphism in insects. Annual Review of Entomology 42:207–230.

Table 1. Response of population parameters to changes in dispersal parameters. Dots represent population parameter outcomes given various dispersal parameter scenarios. Black dots indicate expected outcomes, grey dots indicate unexpected outcomes (see main text for details).

	Population parameters			
Dispersal parameters	PD↑ λ_0↓	PD↓ λ_0↑	PD↓ λ_0↓	PD↑ λ_0↑
β↑, δ↑	●			
β↓, δ↓		●		
β↑, δ↓	●	●	●	
β↓, δ↑	●	●		●

β, disperser expression; δ, dispersal probability; PD, proportion of dispersers; λ_0, population growth rate

FIGURE LEGENDS

Figure 1. Schematic indicating how a population-level approach and an individual-level approach differ in terms of the individuals that emigrate from a population. The blue blocks indicate individuals that stay in the natal population whilst grey blocks indicate individuals that leave the population.

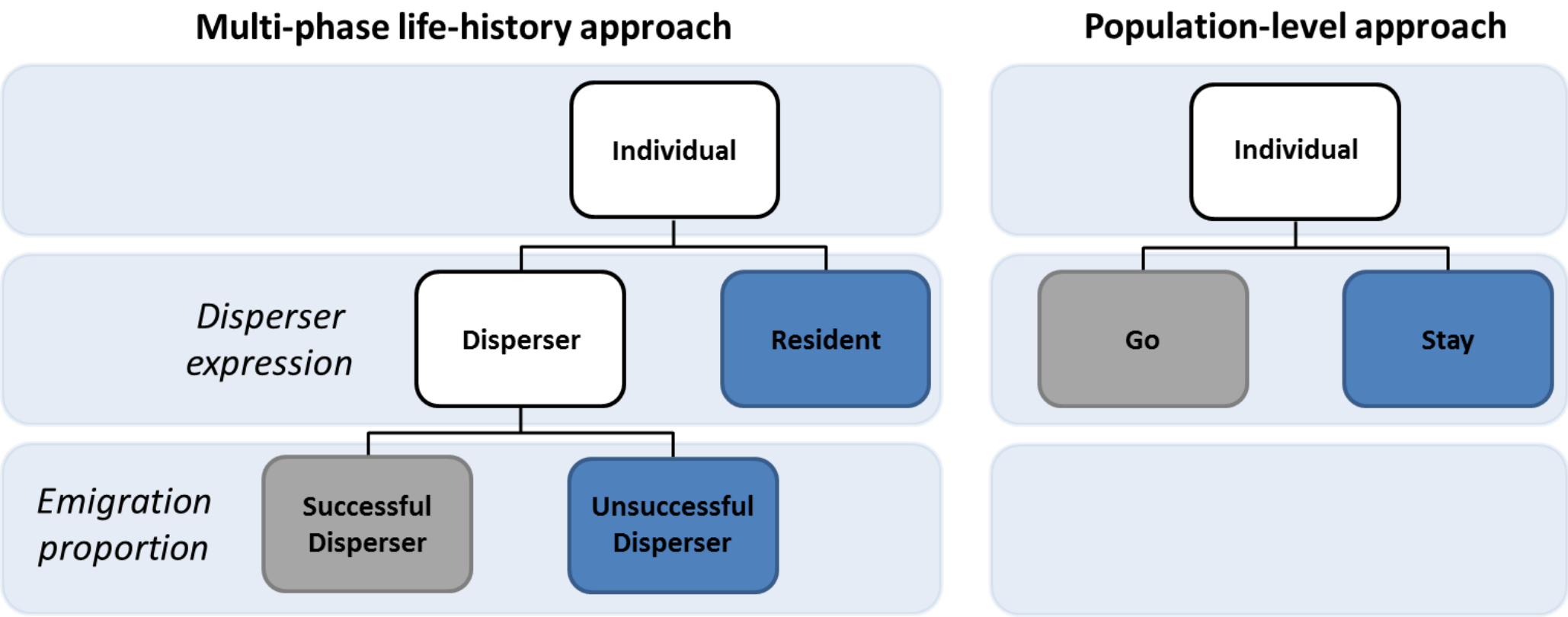
Figure 2. Life cycle of the bulb mite, indicating the six life stages and the vital rates. From the life cycle we calculated the survival (*P*) and fecundity (*F*) rates and the probability of surviving and growing into the next stage (*G*). β indicates the probability of developing into a deutonymph (the dispersal stage).

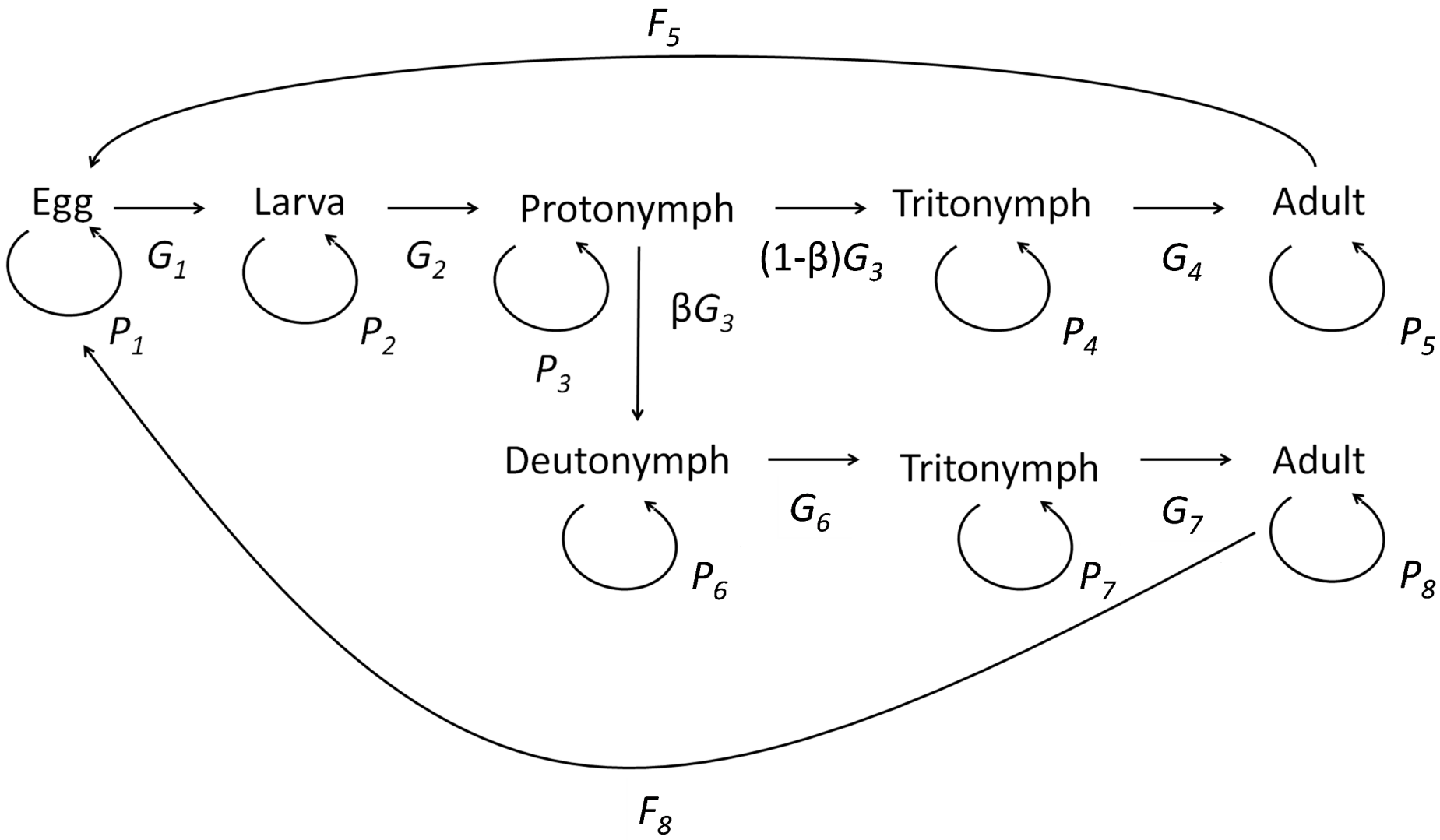
Figure 3. Life cycle of the bulb mite in in the Distinct Disperser Phenotype Model (DDPM) and in the Naïve Model (NM), indicating the life stages and the vital rates. From the life cycles we calculated the survival (*P*) and fecundity (*F*) rates and the probability of surviving and growing into the next stage (*G*). Dispersal in the DDPM consists of development into a disperser (deutonymph) (β) and dispersal out of the population (δ); β describes the transition probability of developing from a protonymph to a deutonymph, δ describes the probability of a deutonymph leaving the population. Dispersal in the Naïve Model (NM) consists of dispersal out of the population (γ); γ describes the probability of any tritonymph leaving the population. See main text for details.

Figure 4. (A) Change in population growth rate, λ_0, with increasing δ dispersal probability. Black lines indicates the response of the Distinct Dispersal Phenotype Model (DDPM) and red lines indicate the response of the Naïve Model (NM) given the γ dispersal probabilities that result in the same proportion of dispersers in both models (see Fig 4B). (B) Change in proportion of dispersers (B) with increasing dispersal probability. Black lines indicates the response of the Distinct Dispersal Phenotype Model (DDPM) with increasing δ dispersal probability and red lines indicate the response of the Naïve Model (NM) with increasing γ dispersal probability. Dispersal probability increases from 0 to 1 at 0.01 increments.

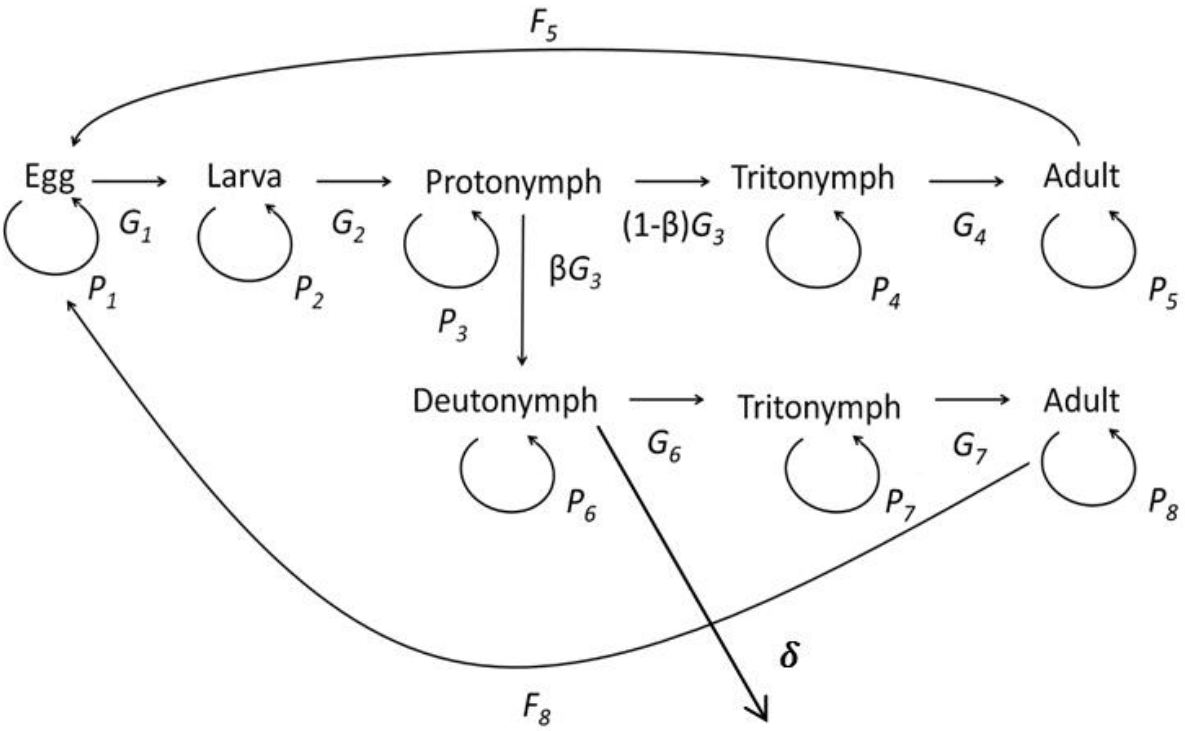
Figure 5. Joint effect of increasing deutonymph frequency (β) and increasing dispersal probability (δ) on the proportion of dispersers. Dispersal probability and deutonymph frequency increase from 0 to 1 at 0.01 increments. Side bar indicates proportion of dispersers with proportion increasing from dark to light green. Coloured contour lines highlight a fixed proportion of dispersers, each proportion can be attained by a number of different δ and β values: 0.04 (yellow line), 0.08 (red line), 0.12 (blue line).

Figure 6. Joint effect of increasing deutonymph frequency (β) and increasing dispersal probability (δ) on population growth rate (λ_0). Dispersal probability and deutonymph frequency increase from 0 to 1 at 0.01 increments. Side bar indicates λ_0, with λ_0 increasing from black to white. Coloured contour lines highlight a fixed proportion of dispersers (0.04, yellow line; 0.08, red line; 0.12, blue line), each proportion can result in a number of different λ_0 values.

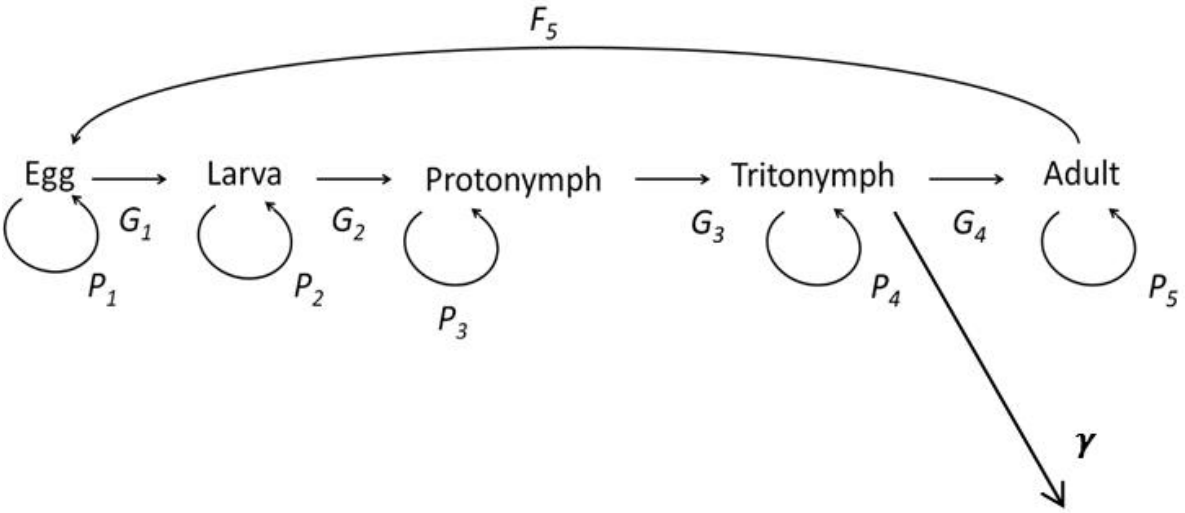

Multi-phase life-history approach
Population-level approach
Individual
Disperser expression
Disperser
Resident
Emigration proportion
Successful Disperser
Unsuccessful Disperser
Individual
Go
Stay

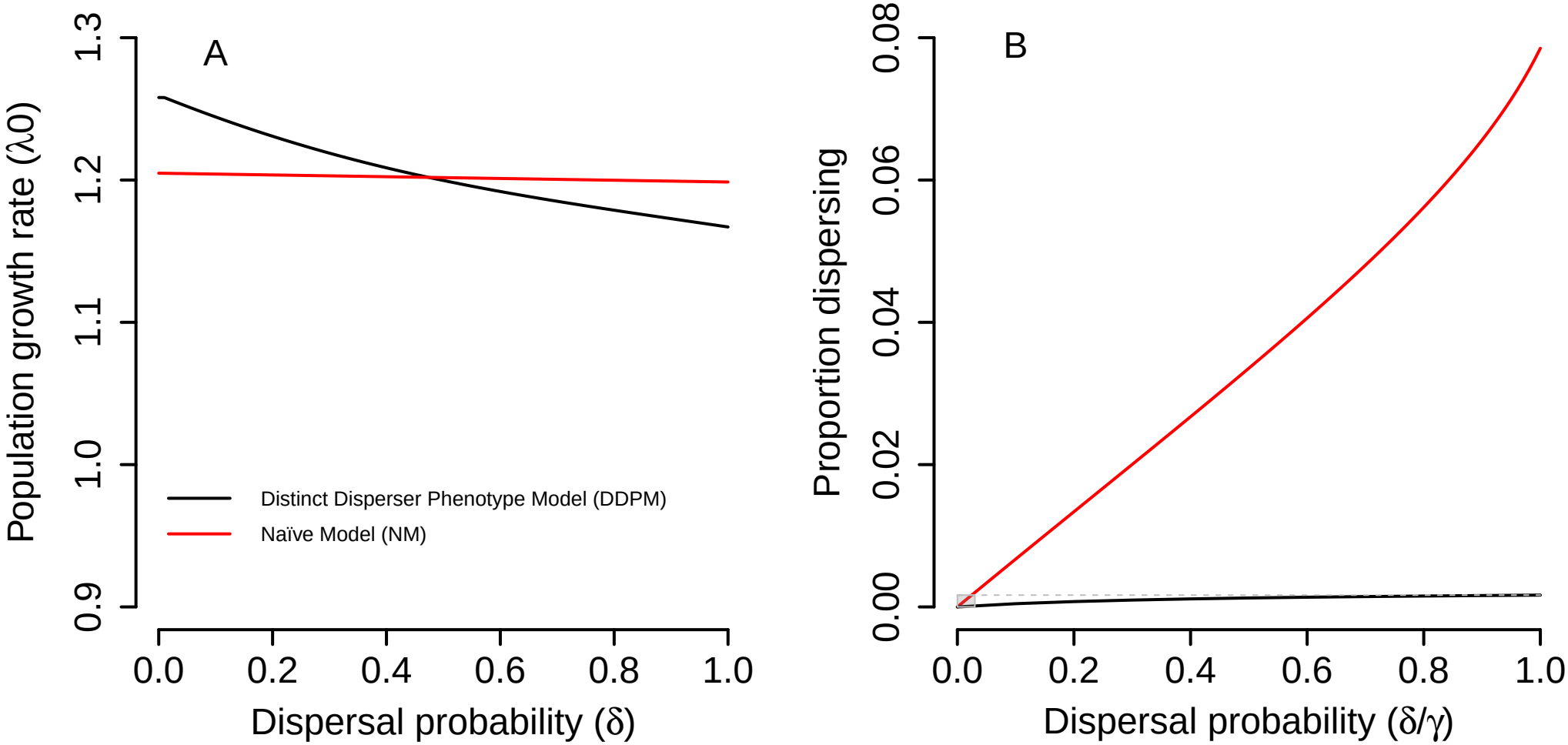

F5
Egg
Larva
Protonymph
Tritonymph
Adult
G1
G2
(1-β)G3
G4
P1
P2
P3
P4
P5
βG3
Deutonymph
Tritonymph
Adult
G6
G7
P6
P7
P8
F8

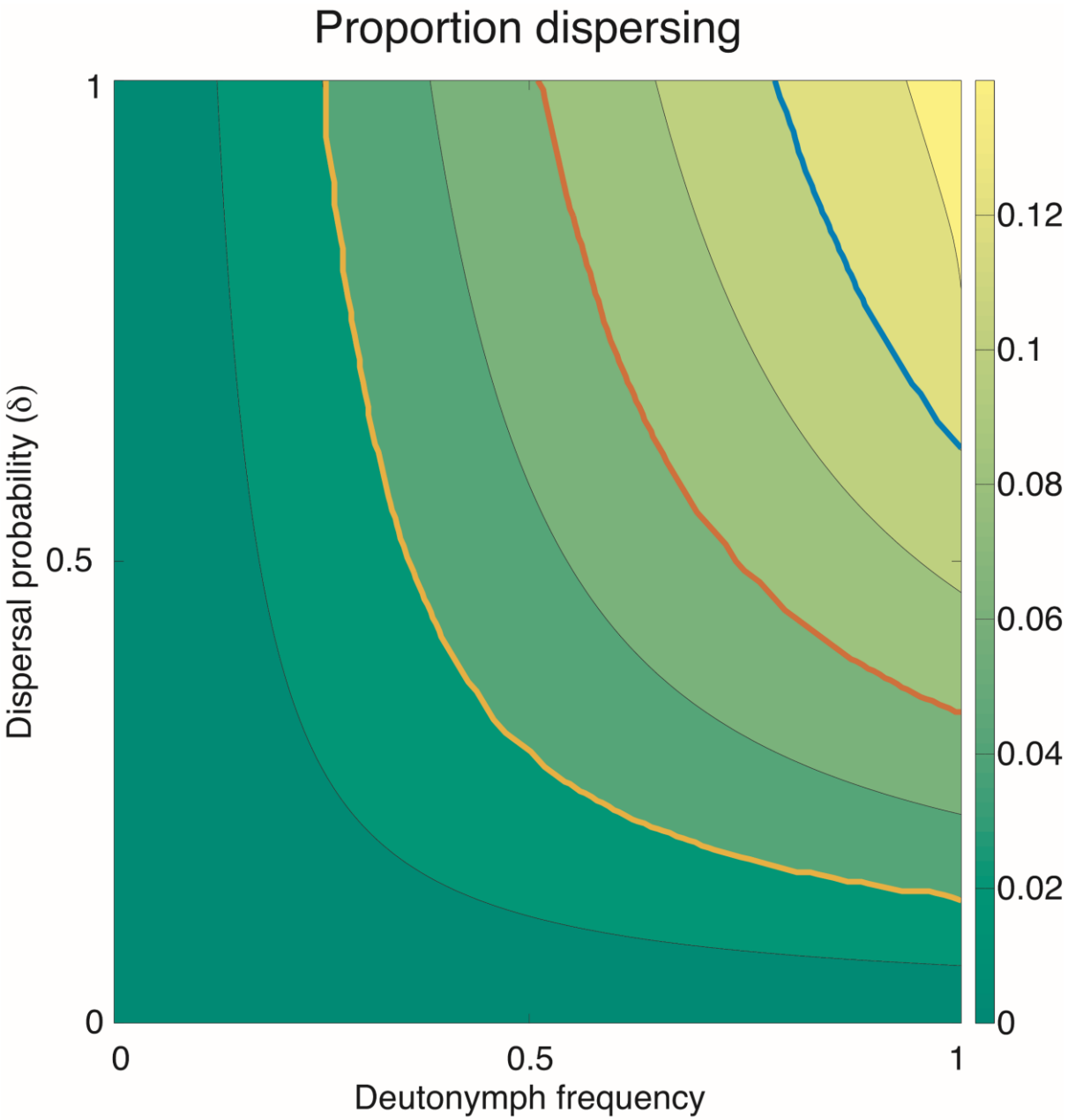
Distinct Disperser Phenotype Model (DDPM)

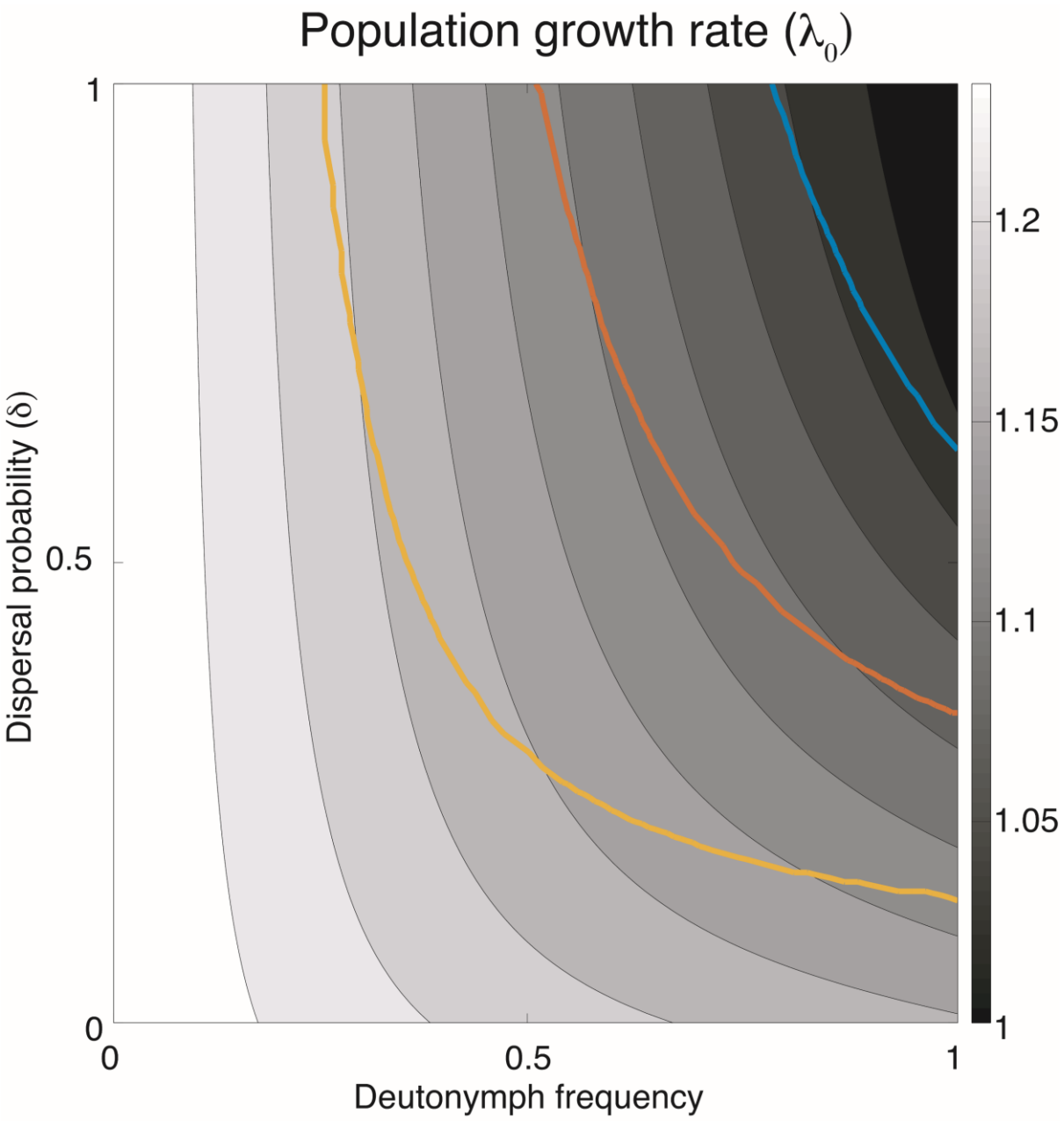


Naïve Model (NM)




A
Population growth rate (λ0)
1.3
1.2
1.1
1.0
0.9
Distinct Disperser Phenotype Model (DDPM)
Naïve Model (NM)
0.0
0.2
0.4
0.6
0.8
1.0
Dispersal probability (δ)
B
Proportion dispersing
0.08
0.06
0.04
0.02
0.00
0.0
0.2
0.4
0.6
0.8
1.0
Dispersal probability (δ/γ)


Proportion dispersing
Dispersal probability (δ)
Deutonymph frequency
0
0.5
1
0
0.5
1
0
0.02
0.04
0.06
0.08
0.1
0.12


Population growth rate (λ_0)
Dispersal probability (δ)
Deutonymph frequency
0
0.5
1
0
0.5
1
1.2
1.15
1.1
1.05
1