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# Eco-evolutionary dynamics of density-dependence along pushed expansion fronts

Chloé Guicharnaud

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# THÈSE DE DOCTORAT

## Dynamiques éco-évolutives de la densité-dépendance au sein des fronts d'expansion poussés

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**Présentée en vue de l'obtention  
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Interactions et Ecologie  
d'Université Côte d'Azur

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# Eco-evolutionary dynamics of density-dependence along pushed expansion fronts

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Dynamiques éco-évolutives de la densité-dépendance  
au sein des fronts d'expansion poussés

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## Résumé de la thèse

La densité de population, c'est-à-dire le nombre d'individus présents dans un espace donné, a une grande influence sur les performances des individus et populations. La présence générale de densité-dépendance et de traits densité-dépendants au sein de l'arbre du vivant fait qu'il est important d'en savoir plus sur comment cette densité-dépendance peut évoluer et influencer les dynamiques de populations. Quand une population se propage dans l'espace, la densité de population peut dramatiquement varier sur une courte échelle spatiale, allant d'un cœur déjà occupé et parfois densément peuplé, aux zones vides au-delà du bord de l'expansion. Dans ce contexte, comprendre comment les traits liés à la dispersion répondent à la densité est essentiel car cela pourrait potentiellement changer les dynamiques écologiques et évolutives le long d'une expansion. Notamment, la densité-dépendance positive au niveau de la dispersion (ou du taux de croissance de la population) peut générer des expansions dites « poussées », où les individus provenant de populations éloignées du front sont la force motrice de l'expansion. Ces dynamiques sont comparées à des expansions plus « tirées » pour lesquelles la propagation est dirigée par les individus au bord du front d'expansion. Beaucoup d'études sur ce continuum tiré/poussé ignorent la possibilité d'une évolution de la densité-dépendance positive, mais aussi comment les traits générant cette densité-dépendance peuvent être corrélés, entre eux ou à d'autres traits. Au cours de cette thèse, j'ai combiné expansions expérimentales et simulées afin d'explorer comment l'évolution de traits d'histoire de vie corrélés et densité-dépendants peuvent influencer les dynamiques éco-évolutives d'un point de vue tiré/poussé. Tout d'abord, j'ai démontré que pour différentes espèces de trichogrammes, des micro-hyménoptères parasitoïdes, la position sur l'axe d'histoire de vie dit du Train-de-Vie (ou *Pace-of-Life* en anglais) était partiellement corrélée avec le statut poussé ou tiré d'une expansion, l'espèce plus « lente » générant des expansions plus poussées. Ensuite, à l'aide de Modèles Individus-Centrés, j'ai trouvé, contrairement à mes hypothèses, que la force de la corrélation entre traits d'histoire de vie n'influence pas de façon significative les dynamiques tirées/poussées globales. Cependant, les coûts de la dispersion peuvent remodeler de façon marquée la relation entre la diversité génétique et la densité-dépendance, un lien clé au sein des dynamiques poussées. Enfin, de nouveau à l'aide d'expansions simulées, j'ai tenté de construire des modèles prédictifs pour inférer des paramètres clés d'expansions poussées, à partir d'un ensemble de métriques basées sur la génétique ou la démographie des populations. Ces métriques seraient facilement récupérables sur le terrain ou à partir de jeux de données empiriques. Notre première preuve de concept présente des résultats encourageants, avec des modèles ayant de bonnes performances pour prédire la présence de densité-dépendance positive sur la dispersion ou une mesure spatiale de la diversité génétique neutre. Globalement, cette thèse démontre l'importance d'inclure l'évolution des traits densité-dépendants au sein des études sur les expansions biologiques tirées versus poussées, car cela pourrait amener à des changements de dynamiques tirées/poussées ; l'histoire (co-)évolutive semble aussi avoir un effet sur le statut poussé ou tiré d'une expansion, ce qui n'est pas le cas pour la structure de la corrélation. Des indications de trajectoires évolutives divergentes entre les expansions poussées générées par de la densité-dépendance positive sur la dispersion ou la croissance de la population ouvre la porte à de futures études sur l'évolution des expansions biologiques, et comment inclure cette évolution afin de réaliser de meilleures prédictions sur des scénarios d'expansions réelles.

Mots clés : Biologie des populations ; Ecologie ; Evolution ; Modélisation

## Thesis Abstract

Population density, i.e. the number of individuals present in a given space, has a major influence on individual performance and ultimately population biology. The nearly ubiquitous presence of density-dependence and density-dependent traits within the Tree of Life makes it important to know more about how density-dependence can evolve and influence population dynamics. When a population is expanding over space, density varies dramatically over a short spatial scale from the already occupied, sometimes densely populated, core area to the empty spaces beyond the expanding edge. In this context, understanding how dispersal traits respond to density is essential to know as it will potentially lead to or shape various ecological and evolutionary changes along the expansion. Notably, positive density-dependence in dispersal (but also in population growth rates) can generate so-called "pushed" expansions, where individuals in populations well behind the leading edge mostly drive the spread. Such dynamics are compared to more "pulled" expansions, in which the spread is driven by individuals at the leading edge. Many studies on this pushed/pulled continuum ignore the possibility of an evolving positive density dependence, and how traits driving that density dependence may be correlated with other traits or each other. During this thesis, I combined experimental and simulated expansions to explore how the evolution of correlated density-dependent life-history traits could influence eco-evolutionary dynamics under the lens of pushed/pulled dynamics. First, I demonstrated that among different species of *Trichogramma* microwasps, each species' position on a pace-of-life continuum was partially correlated with how pushed or pulled the expansion is. Slower species generating more pushed expansions. Then, using an Individual-Based Model, I found, conversely to my expectations, that the strength of life-history trait correlation does not significantly influence overall pushed/pulled dynamics. However, there is evidence that dispersal costs can markedly reshape the relationship between neutral genetic diversity and density-dependence that is key to pushed dynamics. Finally, using simulated expansions again, I attempted to build predictive models that can infer key pushed expansion parameters from a set of metrics based on population genetics or demography that could be easily obtainable from empirical datasets or in the field. Our first proof of concept presented encouraging results, with good model performances when predicting the presence of positive density-dependence in dispersal or the spatial neutral genetic diversity. Overall, this thesis presents the importance of including the evolution of density-dependent traits within studies on pulled versus pushed expansions, as it may result in shifts within this continuum. The (co)evolutionary history also seems to influence how much the expansion is pushed or pulled, but not the correlation structure itself. Indications of divergent evolutionary trajectories between pushed expansions generated by positive density-dependence in dispersal or population growth open the door for further studies on the evolution of biological expansions, and on how to include it to make better predictions in real-life scenarios.

Keywords: Population Biology ; Ecology ; Evolution ; Modelling



'All you need to know for the moment is that the universe  
is a lot more complicated than you might think,  
even if you start from a position of thinking  
it's pretty damn complicated in the first place'  
- **Douglas Adam, *The Hitchhiker's Guide to the Galaxy***





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If I'm being honest, writing this section might have been one of the hardest things I've done. This difficulty lies in my sheer gratitude for all the people who helped, encouraged, reassured, and bared with me for the duration of my thesis. There is not enough place in a reasonable number of acknowledgement pages to accurately share with words how thankful I am to everyone, but I'll do my best!

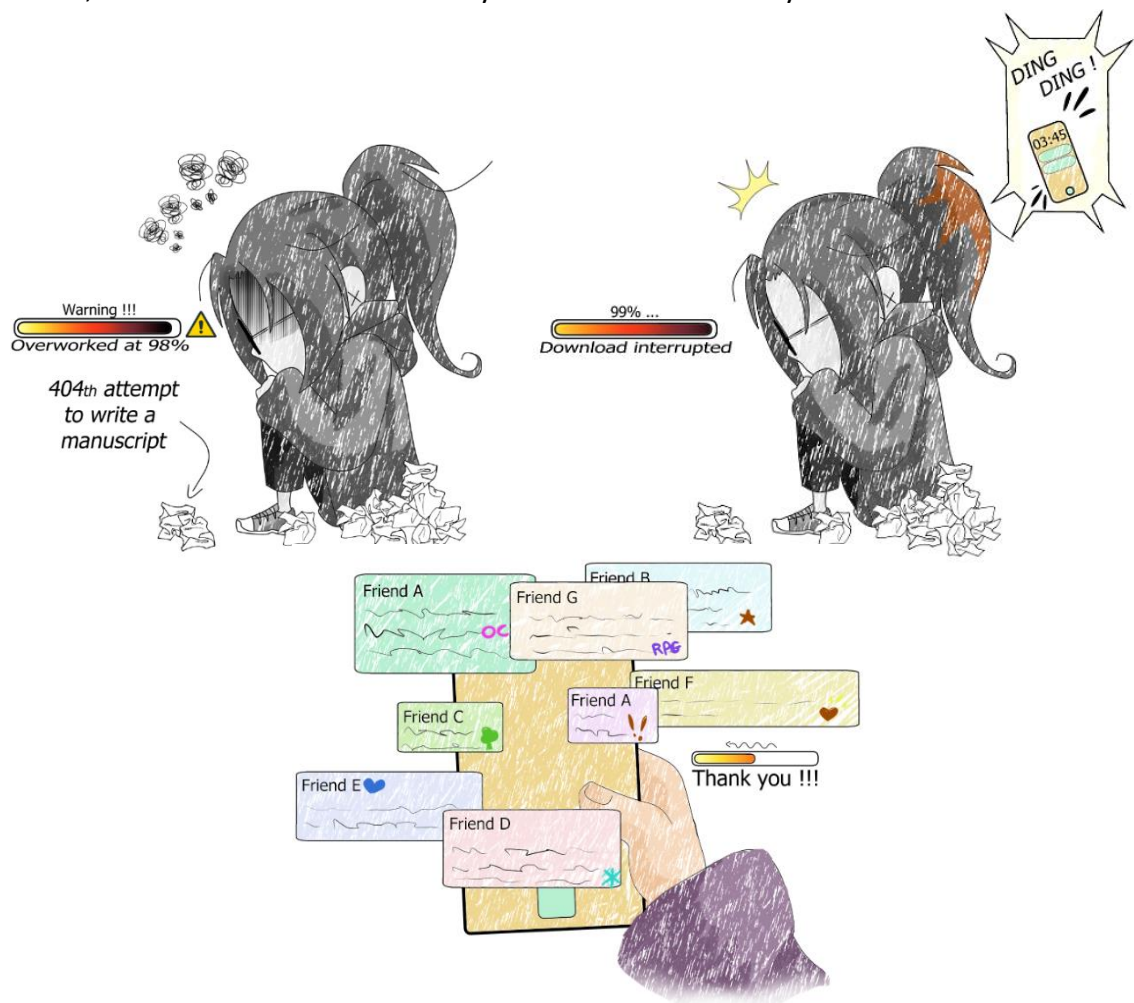
It might be stereotypical of me, but I'd like to dedicate the first paragraphs to my family. Since the beginning, they were there, always behind me. My parents told me they were proud of me when I started this three-year-long journey. Mom and Dad, I am so grateful to you and all you have done for me. Thank you for all those phone calls when my work was too stressful; thank you for your ever-present listening ear and patient understanding; thank you for being there. Even with 900 kilometres separating us, I've never felt isolated or unsupported. I would also like to thank my siblings for all those funny moments and the possibility to take a break from work: little homemade meals with Louis where chemistry and Lord of the Rings meet and merge, awesome cooperation games full of silly (or not) discussions with Gabriel, sparse but funny messages with Thomas, talking science and how complex the educational system is with Tristan and animated debates on which colour is the best with Elisabeth.



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On that note, it is time to end this section. Now, we will embark on a ride I have worked on for three years, with the help and support of everyone I have cited above. If you are ready, please buckle up and prepare a good cup of tea/coffee/water/whatever you need, and here we go!





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I- General introduction:  
Density dependence and population expansions, two  
complex processes interconnected through eco-  
evolutionary feedbacks

## A- You are not alone: What about density?

### A.1- The notion of density

When discussing "density", many definitions can come to mind, as many fields use this term, but with slight variations in its meaning. Density represents the ratio between a measurable quantity and one unit, such as volume or mass. In our case, "density" refers to the number of individuals per discrete unit of geographic area (Schowalter, 2016) and is specifically called "population density". This notion of density is used when looking at the human population within a city (Hawley, 1972; McFarlane, 2016; Greenberg & Schneider, 2023) or when animal population densities are estimated in conservation biology (Dawson & Efford, 2009; Küsel et al., 2011; Twining et al., 2022). We will interchangeably use the terms density and population density throughout this manuscript.

If we look at density as a response and not a causal agent resulting in population changes (McArdle, 2013), either the numerator or denominator can vary and result in a variation in the value of density. From a demographic standpoint, we can have a disequilibrium between the birth rate and mortality rate, when the number of juveniles does not match the number of individuals that died, resulting in a change in population size (Lebreton et al., 1992; McPeck & Peckarsky, 1998). Adding or removing individuals can also be the result of migration or dispersal to or from one delimited area and another way to affect population size (Aghamohammadi & Khorrami, 2022). As presented in Ronce (2007), dispersal will be defined as any movement of individuals that could potentially lead to a gene flow across space.

A variation in the denominator will be related to a change in the geographical area. The more direct approach could be a variation in the surface unit, likened to a reduction or expansion in one population habitat range. However, the quality of habitat, for similar area units, can also affect density (Lin & Batzli, 2001). It is based on the principle that one location can be more or less well exploited by a population and can be similar to the idea of a saturation level, one of the precursors to the carrying capacity (Dhondt, 1988; Zhang et al., 2021). Through time, the habitat quality can deteriorate and lead to a decline in

density (Reijnen et al., 1996), or improve and increase density (mainly observed in successful management plans e.g. Lamb et al., 2018).

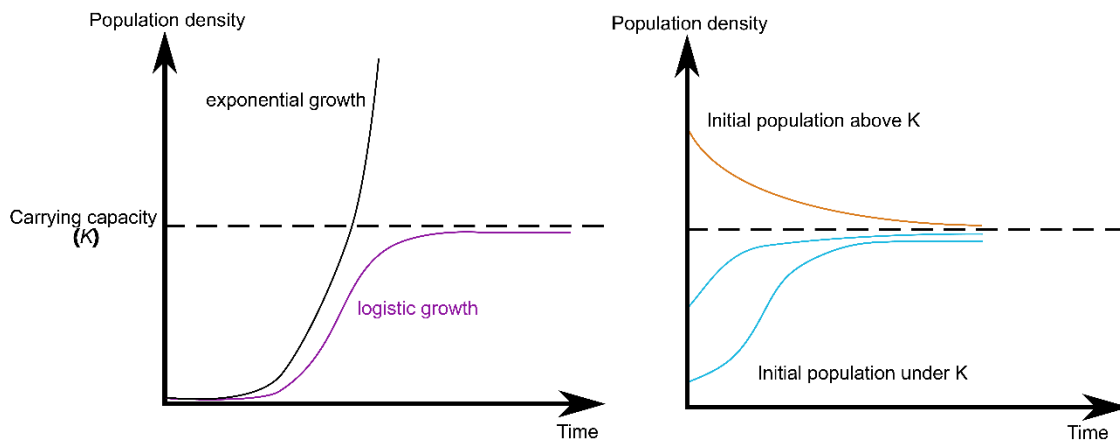
## A.2- Density dependence

Population density is an important variable to know, especially as many traits are density-dependent, meaning that individual trait values may vary depending on the surrounding density (Murray, 1982; Lebreton, 2009). Such cases have been found across the Tree of Life (Fowler, 1987; Stiling, 1987; Holyoak, 1993; Applebaum & Heifetz, 1999; Rose et al., 2001; Leão et al., 2018; Postma et al., 2021; Fiegna et al., 2023), demonstrating the commonality of such phenomena and the need to understand their causes and consequences. While many individual traits or population characteristics can be density-dependent, we will focus on two of them: growth and dispersal.

### *Density dependence in population growth*

Population growth rate corresponds to the rate at which a population increases or decreases for a given time. There is a long history of observing, analysing, and predicting population growth rates, starting long before the 20<sup>th</sup> century when this field really started to grow, no pun intended (Kingsland, 1995). We can cite the Fibonacci sequence (1202) for an unrealistic rabbit population growth or the Malthusian Law (i.e. exponential law, **Figure I.1**) at the end of the 18<sup>th</sup> century. Exponential growth assumes that a population growth rate per individual (or *per capita* growth rate) stays fixed no matter the density, making one population grow increasingly faster as time passes. Without retelling the whole history of population growth models, exponential growth was found to fit census data for specific situations such as at the start of small population growth or in bacterial cultures (Hagen, 2010), but otherwise insufficient. In logistic growth models (**Figure I.1**), we assume that one population can grow until it reaches a density threshold, also called carrying capacity. This threshold is linked to one habitat's limited capacity to sustain individuals. The notion of carrying capacity is rather simplistic as this threshold can and will vary in time and space and is still rather controversial (Del Monte-Luna et al., 2004; Chapman & Byron, 2018). However it can help us visualise the idea that, one population

will tend toward one specific density in response to limited resources (**Figure I.1**). When the population density exceeds this density threshold, we will observe a decline in growth.



**Figure I.1: Comparing exponential and logistic growth**

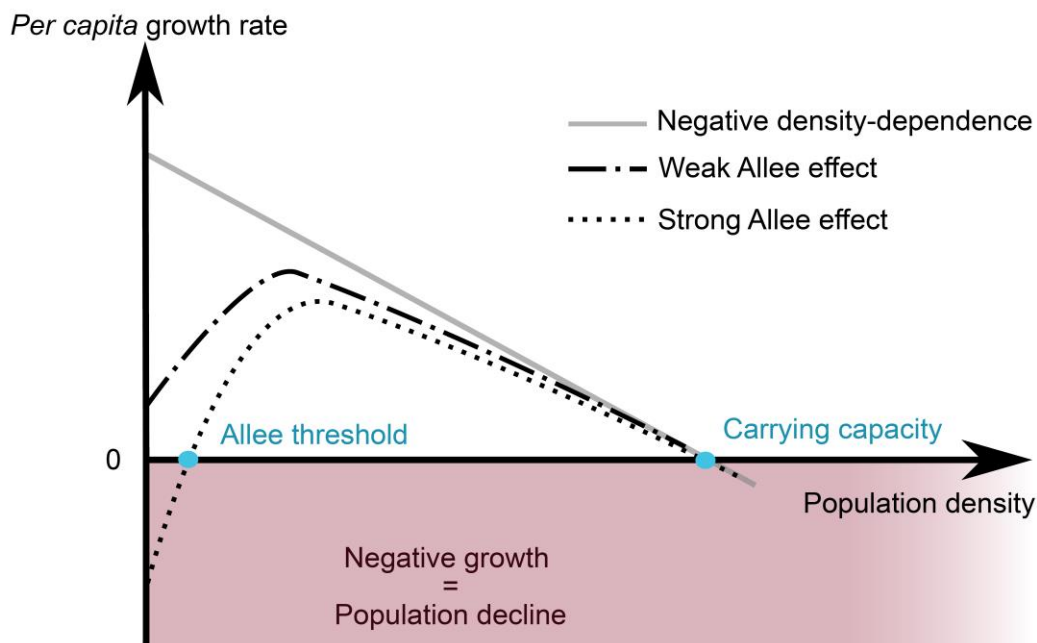
including a density threshold (carrying capacity  $K$ ) on the left, and the asymptotic nature of logistic growth around said carrying capacity no matter the initial population density on the right. Graphs modified from Hartvigsen (2001) and Murray (2002).

Models including such ideas therefore assumed the presence of negative density dependence in growth, with a decline in *per capita* growth rate as density increases. The causes can be multiple: we can have intraspecific competition (Miller, 1967; Petranka & Sih, 1986; Petersson & Järvi, 2000), where conspecific density either decreases the resource's part one individual can acquire (scramble competition) or does not allow to have access to said resource (contest competition). We can also have interspecific competition through interactions with other species' densities (Chesson, 2000; Fricke & Wright, 2017). Finally, we can talk about negative density dependence through frequency-dependent predation (Whelan et al., 2003; Romo et al., 2004), which relates to the fact that predators tend to find high-frequency prey more easily than others less present in the habitat. Because of resource limitations and all the mechanisms favouring it, negative density dependence in growth is nearly ubiquitous.

However, cases of positive density dependence can also be observed, where low densities lead to a population decline (Shilin et al., 1983; Fiegna et al., 2023). This phenomenon was first described and analysed by W.C. Allee, who worked on finding why we observed animal aggregations in nature (Allee, 1931; Allee & Rosenthal, 1948). Not long after, the term "Allee effect", was created by Odum (Odum, 2013). Since then, many studies investigated Allee effects, on a variety of taxa (Stephens et al., 1999; Kramer et al., 2009;

Luque et al., 2013; Kaul et al., 2016; Perälä & Kuparinen, 2017; Angulo et al., 2018; Blackwood et al., 2018; Vercken et al., 2021). Nowadays, we use the term "component Allee effect" to describe the positive density dependence of any measurable component of individual fitness (Courchamp et al., 2008), such as offspring survival, fecundity or female mating success (Matter & Roland, 2013). Component Allee effects are well-studied, both alone (Bourbeau-Lemieux et al., 2011; Matter & Roland, 2013; Kumar & Mandal, 2022) or when interacting together (Multiple Allee effect, Berec et al., 2007; Xia et al., 2013; González-Olivares & Flores, 2015; Tiwari et al., 2020). The positive relation between the overall population growth rate and population density is called the demographic Allee effect. Documenting demographic Allee effects is often more complicated than component Allee effect, and the presence of one component Allee effect does not always mean that there will be a demographic Allee effect (Courchamp et al., 2008; Gregory et al., 2010; Kramer et al., 2018). In this thesis, we will be mainly interested in the population growth rate; therefore, all further mentions of "Allee effect" will correspond to the demographic Allee effect unless specified otherwise.

A demographic Allee effect can be generated through multiple mechanisms, such as a decrease in intraspecific cooperation exceeding the benefits of low competition (Ross-Gillespie et al., 2009), difficulty in finding a mate at low density or other reproductive benefits of being numerous (Hearn et al., 1996; Gascoigne et al., 2009), lesser protection against predators (Gascoigne & Lipcius, 2004; Wormald et al., 2013), higher stochasticity (Lande, 1998; Lee et al., 2011) or inbreeding depression (Willi et al., 2013; Wittmann et al., 2018). The strength of the Allee effect can vary, and we can distinguish two scenarios: on one hand, strong Allee effects, where we do observe negative growth rates under a certain density value (known as the Allee threshold), leading to the inevitable extinction of the population if left alone. On the other hand, while we do observe for weak Allee effects a decrease in growth rate in lower densities, the growth rate remains positive across the range densities (Courchamp et al., 2008)([Figure I.2](#)).

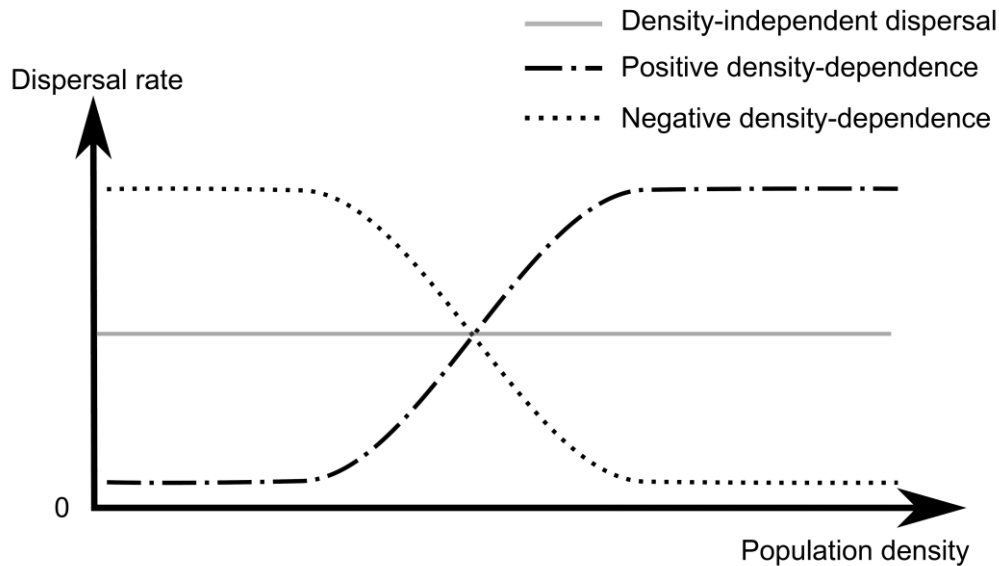


**Figure I.2: Schematic representation of weak and strong Allee effect compared to negative density dependence.**

Modified from Courchamp et al. (2008). When an Allee effect is present, it is generally associated with negative density dependence in growth, and the balance between the two will determine the form of the bell-shaped curves.

#### *Density-dependence in dispersal*

Dispersal is a central trait in population demography, as the balance of emigration and immigration can contribute to population changes just as much as the balance between births and deaths. Dispersal can also rescue low populations from extinction by bringing in new individuals (Berg et al., 2010; Eriksson et al., 2014) with new genetic diversity against inbreeding depression, called genetic rescue (Ingvarsson, 2001; Tallmon et al., 2004; Hufbauer et al., 2015). Dispersal is often not random (Martorell & Martínez-López, 2014; Marmen et al., 2016; Tournier et al., 2017; Terui et al., 2021; and the many examples cited in Clobert et al., 2012) and is often a way to leave one habitat with non-optimal characteristics toward (maybe) more suitable ones. As a result, just as dispersal may shape population density, the reverse is also true and density may influence dispersal (Figure I.3).



**Figure 1.3: Schematic representation of density-dependence in dispersal.**

Those sigmoids (similar to Kun & Scheuring, 2006) are one of the many functions possibly linking density to dispersal rates in the literature. They are easily implemented functions with a flexibility that could rather well mimic what is observed empirically, including negative density dependence in dispersal. However, other models may be better; among others, Metz and Gyllenberg (2001) observed that the evolutionarily stable strategy was for individuals not to disperse under a density threshold, then immediately always disperse above it. In Hovestadt et al. (2010) compared five different strategies, including the two cited above, and found the best model to be the asymptotic threshold model (rooted in the marginal value theorem) (Poethke & Hovestadt, 2002), with no dispersal until an evolving threshold, then an asymptotic increase toward one.

Many cases of density dependence in dispersal rates are observed in animals or micro-organisms (Matthysen, 2005; Harman et al., 2020) and in plants through seed dissemination (Levin & Kerster, 1969). Similar to population growth, positive and negative density dependence is observed, with many factors favouring one or the other (Duputié & Massol, 2013; Harman et al., 2020). The probability of dispersing also depends on its costs, which represent a considerable factor in decision-making or even the possibility of dispersing (Bonte et al., 2012). While population density can also influence the dispersal kernel – how far will dispersers go (e.g. in Bitume et al., 2013; Jansen et al., 2014) – we chose to focus here on dispersal rates i.e. how probable it is that one individual will leave the habitat. What comes naturally is the idea that one individual will tend to depart from habitats with high population density because of intraspecific competition (Grabowska et al., 2019), or kin competition (Ronce, 2007; Cote & Clobert, 2010) through positive density dependence. However, the principle of negative density dependence in dispersal can also



be reasonably understandable when we just saw above with Allee effects that low densities may not imply a better overall fitness through time. Many factors may be the cause for this negative density dependence, as staying in high-density patches with other individuals can be beneficial through cooperation or reduce Allee effects (Fronhofer et al., 2015), but also because individuals from such habitats may be in too poor condition, negatively impacting capacity to disperse (Baines et al., 2020). We resumed and simplified the main points of this section dedicated to population density and how it can influence traits in **Figure I.4**.

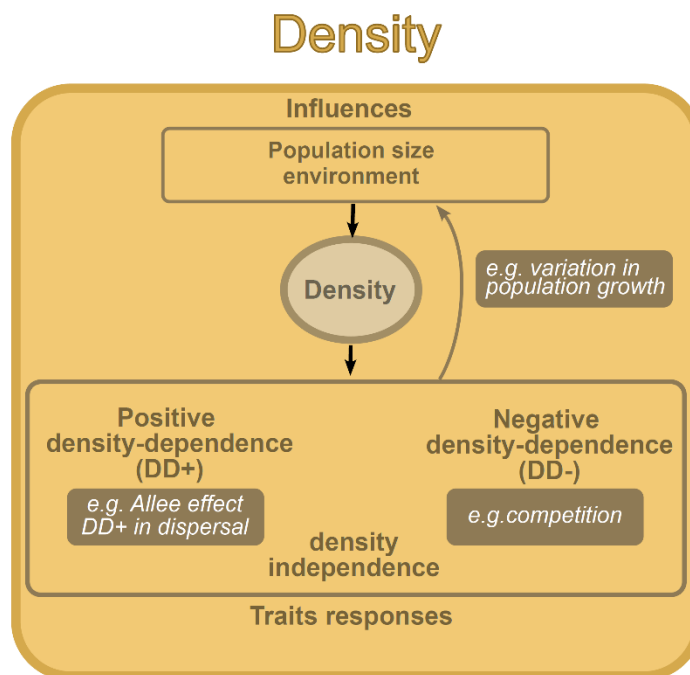


Figure I.4: Schematic summary of population density's effects and influences.

## B- Density influence on evolutionary dynamics and eco-evolutionary feedbacks

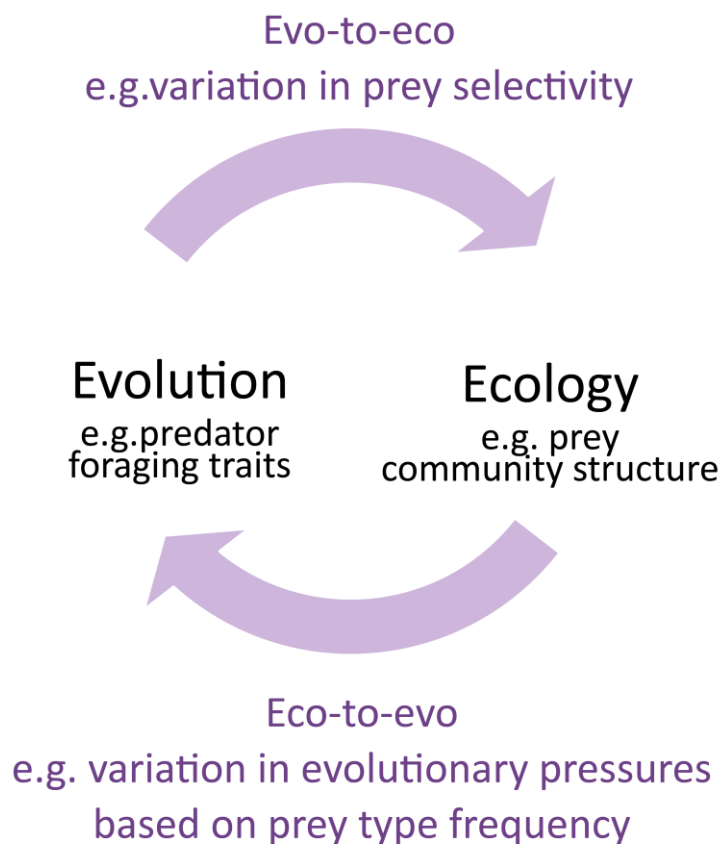
We can also expand our view on density by integrating the notion of evolution and the added complexity that an interaction between the two concepts can have. Indeed, we will see how density can act on selection processes, influence stochasticity, and, in return, be influenced.

## B.1- Let ecology and evolution interact

At first, ecological and evolutionary dynamics tended to be analysed separately, with either unchanged environmental parameters or by removing trait variation and evolution. While the separation greatly simplified studies, it also left the possibility to go straight past interesting influences of one dynamic on the other. Most of the time, it was thought that ecological and evolutionary timescales were too different, making mutual influences negligible (as assumed in Dieckmann & Law, 1996), but it has been proven not to be that much of an issue (Thompson, 1998; Carroll et al., 2007). Quickly, researchers started to incorporate this idea of mutual influence, e.g. with the notion of density-dependent selection (Chitty, 1971). Density-dependent selection is the theory that we observe different traits' evolutionary trajectories depending on population density. Many works have demonstrated the prevalence and importance of density-dependent selection (Mueller, 1997; Whitham et al., 2006; Einum et al., 2008; Travis et al., 2023). This notion is tightly connected to trait density dependence mentioned above as a variation along the density gradient is needed. More indirectly, population density can influence evolution through non-selective processes. Indeed, low densities are more sensitive to stochastic events, such as genetic drift (Buri, 1956; Ellstrand & Elam, 1993), leading to the quick fixation of an allele in such a population.

While the previous paragraph presented the influence of population density on evolutionary dynamics (eco-to-evo, e.g. reviewed in Hendry & Kinnison, 1999; Reznick & Ghalambor, 2001), the relationship between the two is not one-sided and said evolutionary dynamics can also lead to a modification of the ecological patterns (evo-to-eco, e.g. reviewed in Bassar et al., 2010; or Travis et al., 2013). Hanski & Saccheri (2006) presented a correlation between the allelic variation of one candidate gene and the growth of a network's sub-populations of Glanville fritillary butterfly. In a prey-predator system, a shift in the predator's foraging traits (evolutionary process) will result in a shift in prey selectivity (favouring smaller prey, for example); this variation in targeted preys will result in an alteration of prey community structure (Figure I.5). Eco-to-evo and evo-to-eco, when combined, form the core idea of eco-evolutionary feedback (Hendry, 2017, 2023; Govaert et al., 2019; White et al., 2023) (See [Figure I.5](#)). The density-dependent

selection represents only one part of this global research field but demonstrates density's key role in influencing evolutionary processes.



**Figure I.5: Depiction of eco-evolutionary feedbacks.**

This figure represents a narrow view of eco-evolutionary feedback, where one ecological process influences one evolutionary change. However, far more complex feedbacks are possible, incorporating multiple ecological and evolutionary processes, as presented in De Meester et al. (2019). The example presented is based on Palkovacs & Post (2008).

## B.2- You can't have one without the other: Trait correlations through a focus on the pace of life

Integrating multiple traits in an eco-evolutionary study can rapidly add another layer of complexity (Cronin et al., 2020). This complexity can again increase if we remove the simplifying assumption that traits are independent and acknowledge the existence of trait correlations instead. Many processes may cause trait correlations, as presented in Garland et al. (2022). As one individual resource allocation and acquisition is limited (Riska, 1986; van Noordwijk & de Jong, 1986; Laskowski et al., 2021), increasing the value of one trait

might lead to the decrease of another because of a fixed energy pool to draw from (Zhou, 2001). We can also observe genetic links between life-history traits and negative correlations resulting from antagonistic pleiotropic genes or linkage disequilibrium (Sinervo & Svensson, 2002; Bochdanovits & de Jong, 2004; Saggere et al., 2022). Positive or negative correlations force one trait's evolutionary trajectory to depend on another, leading to evolutionary constraints where not all evolutionary trajectories are possible (Stearns, 2000; Prasad & Joshi, 2003; Walworth et al., 2021). One well-known trade-off that is especially relevant for population density is between offspring size and the number of offspring: as resources are limited, investing in bigger offspring (and assuming that size is related to fitness, higher offspring fitness (Krist, 2011; Rollinson & Hutchings, 2013)) leads to a decrease in offspring numbers (Harper et al., 1970; Fox & Czesak, 2000; Ljungström et al., 2016; Dani & Kodandaramaiah, 2017). In another context, the evolutionary process of spatial sorting (Shine et al., 2011) corresponds to the presence of a spatial genetic structure resulting from a variation of dispersal abilities. Individuals with higher dispersal abilities accumulate at range edge and mate with others at the same location, therefore more likely to also have higher dispersal abilities and produce offspring with high dispersal phenotypes. As the main driver behind spatial sorting is an individual's dispersal abilities, this process can be influenced by the correlation between dispersal and other demographic traits (Ochocki et al., 2020; Comerford et al., 2023). In Ochocki et al. (2020), a negative correlation between dispersal and fertility led to a decrease in fertility at range edges.

Which trait combination is selected within a trade-off is often mediated by the environment, including the ecological context, as one combination might be favoured in one specific context and not another (Prasad & Joshi, 2003; Wright et al., 2019, 2020; e.g. Willi & Van Buskirk, 2022; Reyes-Ramírez et al., 2023). In Cope et al. (2021), the authors demonstrated a negative correlation between plant growth and defence against herbivores, where growth was favoured at the cost of weaker defences in environments with high intraspecific competition. As such, life-history trait trade-offs are a good candidate for having important impacts on eco-evolutionary dynamics and their feedback (Martín et al., 2016; Farahpour et al., 2018; Fleischer et al., 2018) (Figure I.6).

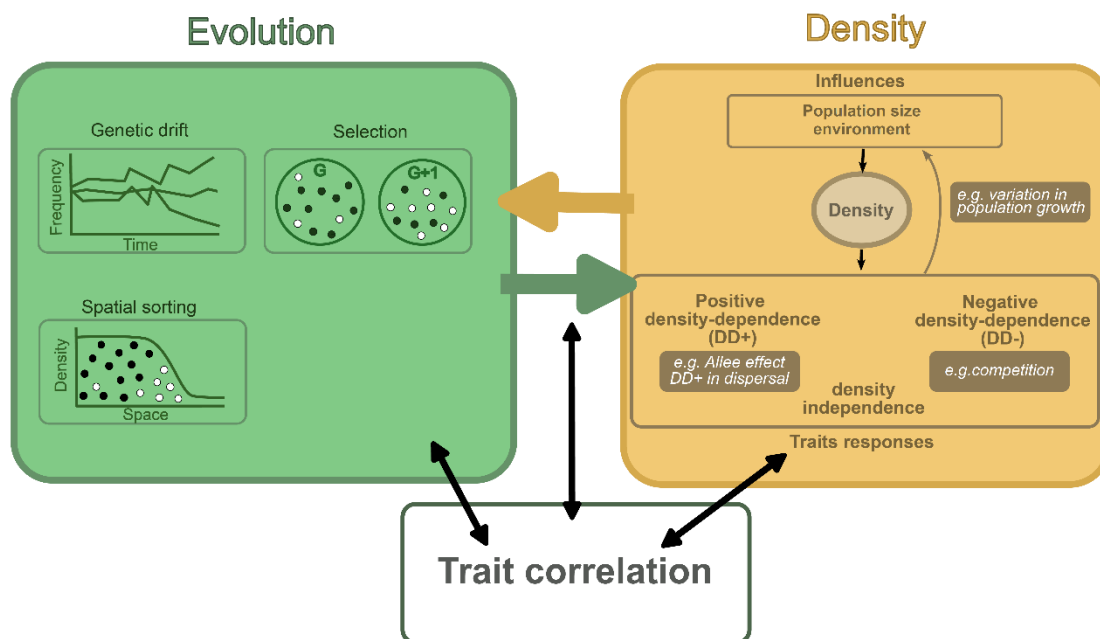


Figure I.6: Schematic summary of evolution and dispersal dynamics along with eco-evolutionary feedbacks.

Major key life-history traits' variation axes can be observed due to trade-offs limiting the range of possibilities, spanning multiple publications and taxa (Gaillard et al., 2016; Healy et al., 2019). One such axis is called the Pace of life. It distinguishes between "slow" species on one end and "fast" species on the other (Stearns, 2000; Braendle et al., 2011). Slow species are characterised by a long development time and longevity but low fecundity and metabolism. In opposition, fast species have short development time and lifespan but higher fecundity and metabolism (Ricklefs & Wikelski, 2002). The pace of life theory can be considered a successor of the  $r/K$  selection theory, with slow species similar to good competitors and fast species as good colonisers. This slow-fast continuum has been mostly analysed and validated at an interspecific level (Blackburn, 1991; Franco & Silvertown, 1997; Bielby et al., 2007; Healy et al., 2019; but see Bakewell et al., 2020). At an intraspecific level, studies on the presence of a pace of life are fewer and more hesitant (Bennett et al., 2002; Nilsen et al., 2009; Réale et al., 2010; Agrawal, 2020; Cayuela et al., 2020). Recently, Wright et al. (2019) reviewed the relationship between the pace of life and density fluctuations. They proposed that slow species or individuals should be better competitors and fare better than fast species/individuals at high densities. Fast species are advantaged at low densities as the higher reproductive output should help with the high-density fluctuations present. Furthermore, pace-of-life axes can be associated with

other traits to form pace-of-life syndromes (Wolf et al., 2007; Réale et al., 2010; Auer et al., 2018). Much is still unknown about the interaction between trait correlations and eco-evolutionary feedback, such as the consequences of correlations between density-dependent traits on eco-evolutionary dynamics within population expansions.

## C- Keep moving forward! Population expansion

Species distribution in space and species ranges are not fixed and can vary over time (Peterson & Lieberman, 2012; Thorson et al., 2016; Rubenstein et al., 2023). We define population expansion as the outward spatial spread of a population of individuals. Expanding populations are structured around a density gradient from a high-density core to a low-density range edge and represent a unique environment in which assumptions made on non-expanding populations do not always hold (Phillips et al., 2010; Shine et al., 2011; Lombaert et al., 2014; Masson et al., 2018). Excoffier et al. (2009), reviewed the genetic differences between a pure demographic increase without spatial expansion and spatial expansions. For instance, increasing the number of individuals without expansion in space should lead to less genetic drift (Kimura & Crow, 1963). However, in spatially expanding populations, intense genetic drift is observed at range edge (Hallatschek et al., 2007) as a result of low densities there. Because of that density gradient, expansions offer interesting conditions for studying the central role of density dependence in evolution, ecology and eco-evolutionary feedback (Sullivan et al., 2017; Birzu et al., 2019).

However, studying biological expansions, i.e., how one species might modify its distribution through diverse mechanisms, has interests outside of this density gradient. It has been the focus of entire fields of studies, each one complementing the other to understand expansions. We can look at how expansions can be generated (reviewed in Facon et al., 2006; Sexton et al., 2009; Estrada et al., 2016), where they started alongside with their invasion routes (Williams et al., 2004; Brown et al., 2011; Wan et al., 2012; Yu et al., 2017; Oficialdegui et al., 2019), what happens during expansions (including eco-evolutionary dynamics) (Excoffier et al., 2009; Peischl et al., 2015; Fronhofer & Altermatt, 2015; Phillips & Perkins, 2019; reviewed in Miller et al., 2020), what are the consequences on the new environment (Phillips et al., 2009; Reichard et al., 2015; Gallardo et al., 2016;

Koorem et al., 2018; Manrubia et al., 2019) or the diverse anthropogenic disturbances (Cook et al., 2007; Madin et al., 2012).

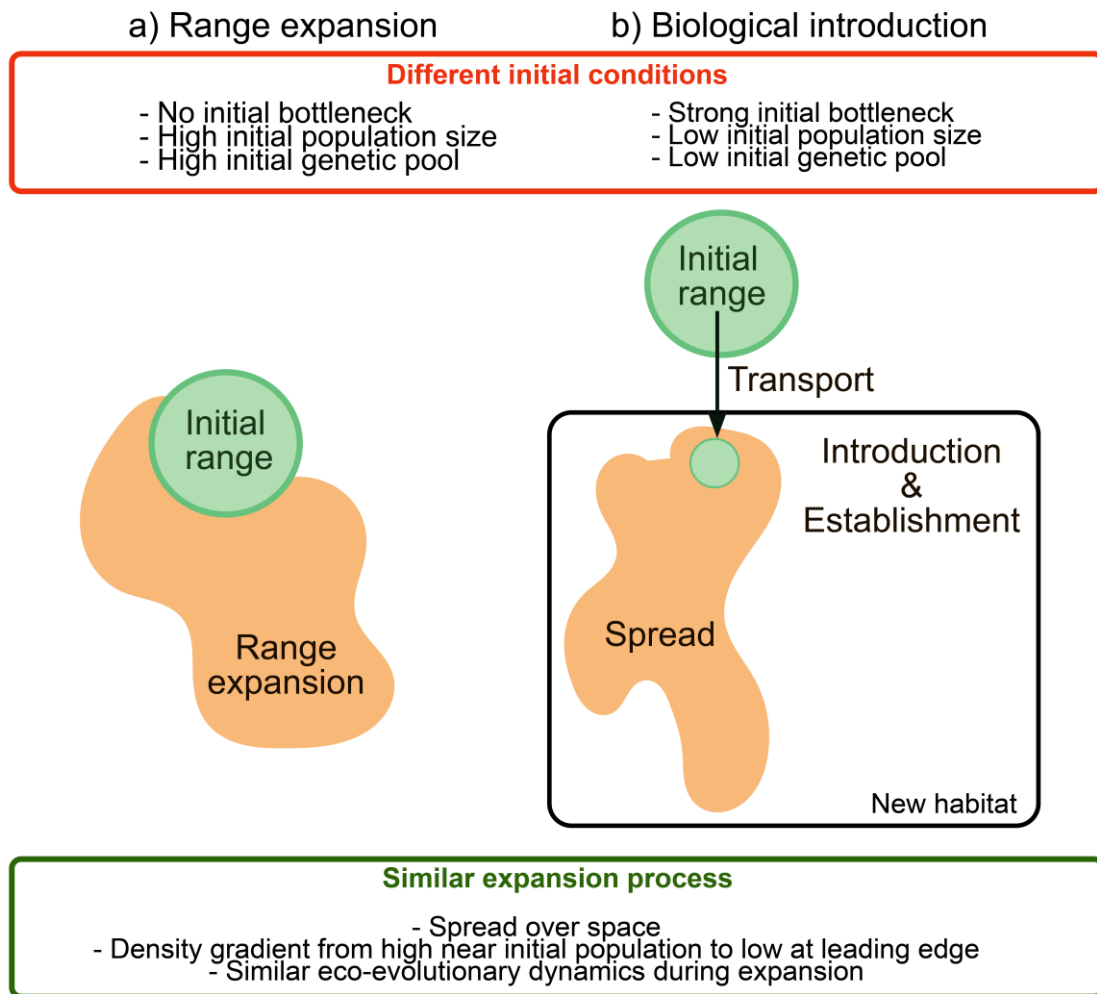
## C.1- Range shifting and introduced species: two expansion starting points

It is possible to distinguish between two categories of population expansions, depending on whether or not a continuity to the original range is observed (**Figure I.7**). On one side, we have the idea of range shifting, where one population will expand (or shrink) its habitat range to new adjacent areas. Range shifting can result from modification of the environment, which somehow favours the colonisation process (Thomas, 2010). Climate change (both natural and human-made) has played an important role in past expansions (Ledoux et al., 2018; Garg et al., 2020) and is also the cause of many range shifts observed nowadays (Lundy et al., 2010; Cunze et al., 2013; Dawe & Boutin, 2016; Farashi & Alizadeh-Noughani, 2023).

On the other side, an expansion can originate from a population introduced into a new suitable habitat. Some populations have been introduced intentionally through management plans (among them *Harmonia axyridis*, for biocontrol purposes, Roy & Wajnberg, 2008) or because of their "exotic" aspect (like sport fishing, Dextrase & Mandrak, 2006) but are now considered as invasives. The introduction can also be non-intentional, mainly through human transportation (Hulme, 2021). There is also the possibility for an introduction and following expansion to be natural, without human intervention (i.e. natural colonisation), which has sparked a debate on whether or not biological invasions and natural colonisations could be considered similar (Hoffmann & Courchamp, 2016; Wilson et al., 2016).

Range shifting and introduced populations may differ by several aspects, some driven by the higher initial population size or gene pool for the former, thanks to the direct connection to the main population. However, I have decided in this thesis to focus on expanding population in general, as many aspects are shared between these two main expansion (**Figure I.7**) (e.g. Sorte et al., 2010b). Unless specified, the terms "expansion" or

"population expansion" will therefore combine range-expansions and introduced expanding populations/biological invasion through the thesis.



**Figure 1.7: Different expansion processes into a new habitat.**

a) Range expansion, with continuity to the initial species' range. b) Biological introduction mediated by (primarily human) transportation leading to the establishment and spread into another suitable habitat disconnected from the initial range. Partially inspired by the IPBES report (2023). Depending on long-distance dispersal, other representations of range expansions can be observed, with more or less connectivity with the initial range (see Shigesada & Kawasaki, 2002).

## C.2- Why study expansions? Effects on the new environment

### *Impacts on diversity and local communities*

Expanding populations will generally modify the ecosystems they arrive into. The presence of a new species can modify community structures (Collins et al., 2016; Aguilera et al., 2020; Qin et al., 2022), the local species diversity (reviewed in Dogra et al., 2010),



or even trophic interactions (Dorcas et al., 2012; Kirk et al., 2022). If the expanding species is an ecosystem engineer, we can observe modifications of local abiotic or biotic conditions, generating cascading effects (reviewed in Crooks, 2002; Guy-Haim et al., 2018; Emery-Butcher et al., 2020). The Sydney golden wattle or *Acacia longifolia* is a species first imported from Australia to Portugal to limit the erosion of coastal habitats but quickly became invasive and caused significant modification in community and soil composition (Marchante et al., 2003, 2008; Rascher et al., 2011). The long-spined sea urchin *Centrostephanus rodgersii* in the east coast of Australia has seen its initial range expand Southward because of climate changes (Davis et al., 2023; but its expansion can also result from overfishing, e.g. Jackson et al., 2001); said sea urchin is also known for transforming kelp forests into sea urchin barrens (Ling, 2009).

Similar expanding species have such impacts on the local ecosystem that 'legacy effects' can subsist even after removing the ecosystem engineer (Cuddington, 2011). In the case of the introduced *A. longifolia*, the modified soil composition is suitable for *A. longifolia*'s seedling growth and some time post-removal, or outside intervention, is needed before the ecosystem returns to favourable conditions for the recolonisation of natal species (Marchante et al., 2009; Le Maitre et al., 2011). A first successful invasion can also modify the ecosystem, such as secondary species invasions are facilitated, leading to "secondary invasions" (O'Loughlin & Green, 2017), amplifying the potential influence of alien species on one ecosystem.

#### *On a more anthropocentric view: costs and economic consequences*

Some population expansions become an issue primarily because of the economic costs or healthcare issues they can generate and require management strategies to mitigate those costs. The mosquitoes *Aedes aegypti* and *Aedes albopictus* have seen their range expand worldwide (Liu-Helmersson et al., 2019; Iwamura et al., 2020), leading to increased *Aedes*-borne virus transmissions (Ryan et al., 2019) and a cumulative economic cost of 87.3 billion US\$ between 1975 and 2020 (according to a preprint by Roiz et al., 2023). As mentioned above, an expanding species may modify (or destroy) its new biotic and abiotic environment. Many reviews can be found about the general costs of biological expansions (mostly invasion-centered), combining management, removal, and indirect economic

costs (Lovell et al., 2006; Olson, 2006; Diagne et al., 2020, 2021; Roy et al., 2023). The damages on the ecosystem and the need for post-expansion modification/restoration are the most costly consequences of an expanding species, with reviews supporting early or pre-expansion management plans as a way to reduce costs (Cuthbert et al., 2022; Ahmed et al., 2022; Vaissière et al., 2022). Assuming nothing more is done to reduce invasive species' number or influence, the total costs will most likely continue to increase, with costs estimated for 2040 in Europe only ranging from 21.1 to 30.6 billion US\$ (Diagne et al., 2021; Henry et al., 2023).

#### *Expansions for classic biological control*

Among the different strategies used to control pest species, biological control agents (predators, parasitoids or microbial agents) represent a double-edged sword to handle with care (De Clercq et al., 2011; Loomans, 2021). Among the three strategies of biocontrol using voluntary and controlled (in theory) introductions of biological agents – classic, inoculation or inundation (Eilenberg et al., 2001) – we focus here on classic biocontrol (CBC). CBC consists in the voluntary introduction of a species with the expectation of permanent establishment. It relies on community-agent interactions, such as only the targeted species is negatively affected. Therefore, CBC requires, in part, the expansion of an introduced population, but only in the expected area. We will see below that in some cases, the expansion process fails or, on the contrary, works so well that the biocontrol agent becomes an invasive species with negative impacts. Knowing how a biocontrol agent will behave and expand once introduced is, therefore, essential for biocontrol strategies.

One success story is the case of the biocontrol by a parasitoid wasp, *Torymus sinensis*, on the chestnut gall wasp *Dryocosmus kuriphilus* used worldwide (Quacchia et al., 2008; Gibbs et al., 2011; Matošević et al., 2017; Borowiec et al., 2018). *Torymus sinensis* expansion follows the invasive range of its highly specific host *Dryocosmus kuriphilus*, without observed negative consequences on the environment (but see Gil-Tapetado et al., 2023). Successful establishment but no subsequent expansion was observed for the weevil *Rhinocyllus conicus* introduced in South Africa in 1984 against the spear thistle *Cirsium vulgare* (Hodson et al., 2003). However, the use of *R. conicus* has become

controversial because of its involuntary negative impacts on other *Cirsium* species (Turner et al., 1987; Rose et al., 2005). Lastly, the expansion worked so well in some cases that the biocontrol agent is now causing more harm than good outside of the expected range. For instance, the cactus moth *Cactoblastis cactorum* was introduced in the Caribbean to reduce prickly pear cacti (genus *Opuntia*) populations. Previously, *C. cactorum* was successfully used in Australia against exotic *Opuntia* (Raghu & Walton, 2007), but when later introduced in the Caribbean, it resulted in an unexpected introduction into mainland America, threatening native *Opuntia* (Johnson & Stiling, 1998; Zimmermann et al., 2000; Zimmermann, 2006; Jezorek et al., 2012).

### C.3- Combining *in natura*, experimental and simulated expansions to understand better biological expansions as a whole

Put together, the increased number of biological invasions detected (The IPBES cited over 37 000 established alien species in their 2023 report; see Roy et al., 2023), the effect of climate change on range expansion (Parmesan & Yohe, 2003; Lenoir & Svenning, 2015), the number of failed management plans, and the possibly dire consequences both for the environment and human economy highlight the need to understand the inside dynamics of population expansion better. By doing so, it would be possible to i) limit the risks (or the adverse effects) of new unwanted expansions, ii) reduce management plan costs by pinpointing the exact mechanism(s) behind an expansion (and therefore the exact leverage points for intervention), and iii) have a better view of species interactions with their biotic and abiotic environment.

Pros and cons can be presented for each approach to study expansions, be it the observation of ongoing biological expansions *in natura*, experimental expansions in the lab with controlled conditions, or simulated expansions using models (see Lustenhouwer et al., 2023 as an example for dispersal studies).

Natural systems offer the possibility to study "real" expansions with all the interactions, possible feedback and complexity it entails. They represent what concretely happens when a population expand. Many methods can be used (and combined) to extract valuable information to track and analyse natural expansions (Kamenova et al., 2017).

However, complications can arise from studying expanding populations through observation of old or ongoing expansions *in natura*. Natural expansions do not happen in a controlled environment; only successful expansions are observed, resulting in an observation bias, and researchers face high variability for few replicates (Nalepa et al., 2010). Many uncontrollable sources influence such expansions, and it can become difficult to pinpoint the exact cause of one observed result (Churchill, 2013). The number of independent replicates is challenging to solve as expansions can substantially impact the environment, and as we just saw, releasing potentially invasive species is not often feasible or wanted. Of course, there are cases of voluntary human-assisted migrations outside the initial species range to more suitable locations (Backus & Baskett, 2021; Twardek et al., 2023) or expansions used for biological control (see above).

Experimental expansions in laboratory settings or mesocosms can help deal with some downsides of natural expansions. First, the environment is more controlled during the expansion process, reducing the sources of variation or stochastic events. By having more control over biotic (e.g., temperature, habitat fragmentation, salinity, Alto & Juliano, 2001; Jaspers et al., 2011; Williams et al., 2016; Fronhofer et al., 2017) and abiotic (e.g. presence/absence of competitors, kin selection, evolution, Williams et al., 2016; Weiss-Lehman et al., 2017; Van Petegem et al., 2018) aspects of expansion dynamics, it is possible to observe the effect of specific expansion drivers, with independent replicates (Morel-Journel et al., 2015; Larsen & Hargreaves, 2020). Such experiments come at the cost of less realism than natural expansions, and the limitations within a laboratory in terms of space and time prevent us from experimenting with large biological models or for an extended period, resulting in non-random taxonomic biases. Some responses can, therefore, only be extrapolated to longer scales with care (Morales & Ellner, 2002; Williams et al., 2016).

Simulated expansions offer complete control over an expansion parametrisation (see e.g. Bocedi et al., 2021 for an example of a flexible software). With that, many scenarios can be analysed and not restricted by the life-history trait values of one biological model (Peischl et al., 2015; Ochocki & Miller, 2017; Dominguez Almela et al., 2020; Urquhart & Williams, 2021). Such expansion results are not influenced by unaccounted-for mechanisms (or only by new emerging properties (Bascompte & Solé, 1995)). One

downside of simulated expansions is that their modelling relies on simplified environments and interactions compared to what experimental or natural expansions can have (Kareiva & Andersen, 1988; but see Peck, 2004). Therefore, simulated expansions can be good for exploring a vast array of hypotheses and theories, but they must be corroborated with new or pre-existing natural and experimental data to confirm their validity and application in biology.

As we just saw, each approach has its weaknesses covered by the strengths of another (Figure I.8). It highlights the necessity to exploit and interconnect experimental, simulated and expansions *in natura* if we want complete coverage of biological expansions (Harrison, 1987; Ochocki et al., 2020; Dahirel, Bertin, Calcagno, et al., 2021; Dahirel, Bertin, Haond, et al., 2021). For instance, we could observe a pattern in wild expansions, identify the causes through simulations, and test our conclusions with experimental expansions to observe whether they are reproducible in semi-realistic conditions.

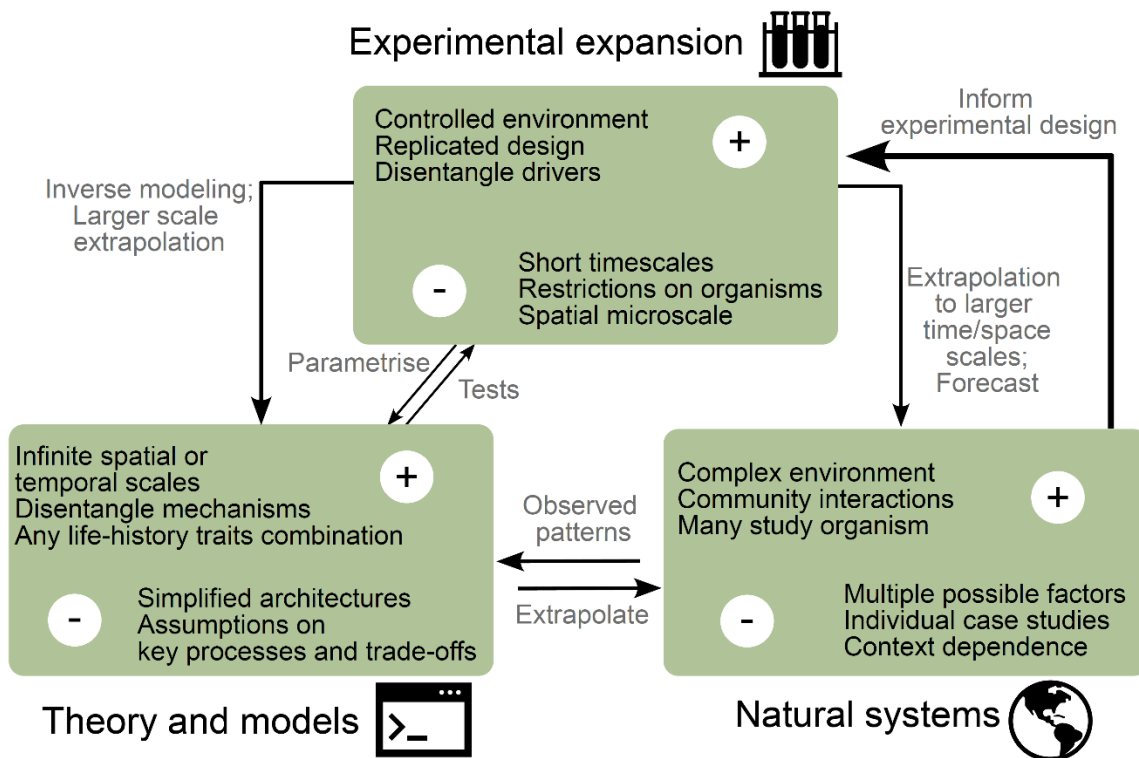


Figure I.8: Links between the three approaches to study expansions

Experimental expansions in the lab, modelled and natural expansions. Adapted from Lustenhouwer et al. (2023).

## D- Density dependence and inside dynamics of biological expansions: Pulled or pushed?

During this introduction, we discussed how significant density dependence is in ecological and evolutionary dynamics. We also discussed population expansions and how they can have important consequences on their new environment and potentially on the human economy. We saw that, through different methods, ecological and evolutionary dynamics in said expansions can be studied. As with other biological processes, population expansions present eco-evolutionary dynamics and feedbacks. This section will present the expected inside dynamics of an expanding population and the non-negligible influence density-dependence in growth or dispersal can have on said dynamics. In the scope of this thesis, we will focus on the inside dynamics of one species in a new empty environment, removing interactions with other species, whether by competition or cooperation.

### D.1- "Classic" ecological and evolutionary dynamics of expansions: Pulled expansions

An expansion is a dynamic process with variations in time and space. A few individuals will disperse ahead and install themselves in a previously empty spot at the leading edge, where the expanding population meets the new empty habitat. This pioneer group becomes the new leading edge, and the process continues to the next empty area. Those steps are the basis of an expansion and generate a succession of less and less dense patches as they get closer to the leading edge, forming a gradual density variation. In mathematics, the concept of travelling waves, particular solutions of reaction-diffusion models where the velocity and the wavefront profile are constant, is an excellent way to represent such expansions. Under such conditions, its spread in time  $t$  and space  $x$ , noted  $u(t, x)$ , can be represented with the differential equation:

$$\frac{\partial u}{\partial t} = \frac{\partial^2}{\partial x^2} (D(u) u) + f(u)$$

With  $\frac{\partial^2}{\partial x^2}(D(u)u)$  the dispersal operator and  $f(u)$  the growth term. The Fisher-KPP model (Kolmogorov et al., 1937; Fisher, 1937) is the first formalisation of such dynamics, and the underlying basis of most models that followed (see Lewis et al., 2016). When an expansion fulfils the assumptions behind the classic Fisher-KPP reaction-diffusion model, its long-term velocity  $v_F$ , can be calculated with the following generalised expression:

$$v_F = 2\sqrt{D(0)r(0)}$$

where  $D(0)$  represents the diffusion rate and  $r(0)$  represents the per capita growth rate, both at density 0 (in practice measured at very low densities).

As these very low densities that determine velocity are typically seen at the leading edge of an expansion, one can conclude that population growth and dispersal at the front edge are the driving forces behind expansions. Expansions that fit this common modelling framework are therefore said to be "pulled" forward by this leading edge. Increased dispersal or growth term should both lead to increased velocity, as corroborated with experimental or natural expansions (for dispersal: Phillips et al., 2008; Lombaert et al., 2014; Weiss-Lehman et al., 2017; for growth rate: Phillips, 2009; Masson et al., 2018).

Among the processes leading to increased growth or dispersal at the range edge is spatial sorting (Shine et al., 2011; Phillips & Perkins, 2019). This spatial equivalent of natural selection plays an essential role during population expansion thanks to the constant density gradient inherent to the process (beautifully explored in Ochocki, 2017). It favours high dispersers at the leading edge, reinforced at each generation with a positive feedback, as the spatial structure makes reproducing between low and high dispersers challenging. Increased velocity by higher growth or dispersal values can also happen thanks to a selection on fitness: High dispersers will tend to move away from high densities, reducing the pressure on individuals in case of negative density dependence, resulting in better fitness (Altwegg et al., 2013; Travis et al., 2013). The two deterministic processes will interact simultaneously within the same expansion (**Figure I.9**) with the addition of other stochastic processes.

During expansion, low-density populations at the range edge can be more prone to genetic drift, as presented in the first section of this introduction (Buri, 1956; Ellstrand &

Elam, 1993). Combined with the spatial aspect of expansions, this may lead to gene surfing. Gene surfing corresponds to an observed frequency increase of one random variant at the leading edge, primarily due to successive bottlenecks. While deterministic processes tend to increase fitness (spatial or temporal), the random fixation of deleterious alleles can also decrease it (Foutel-Rodier & Etheridge, 2020). Neutral genetic diversity is also affected by gene surfing and demonstrates rather well the stochastic aspect of this process (Pierce et al., 2014; Schlichta et al., 2022).

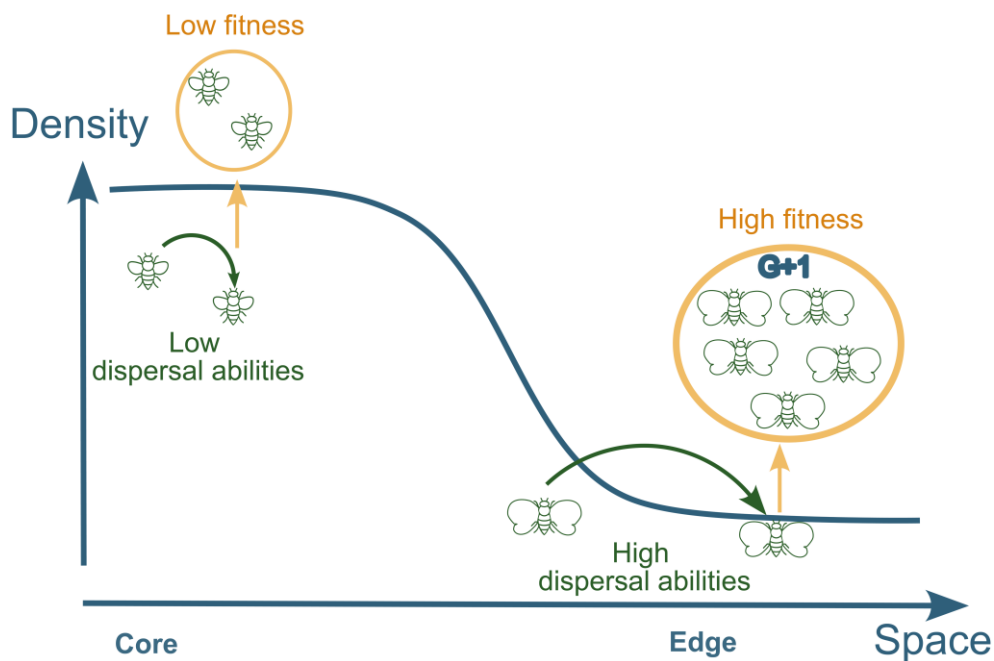
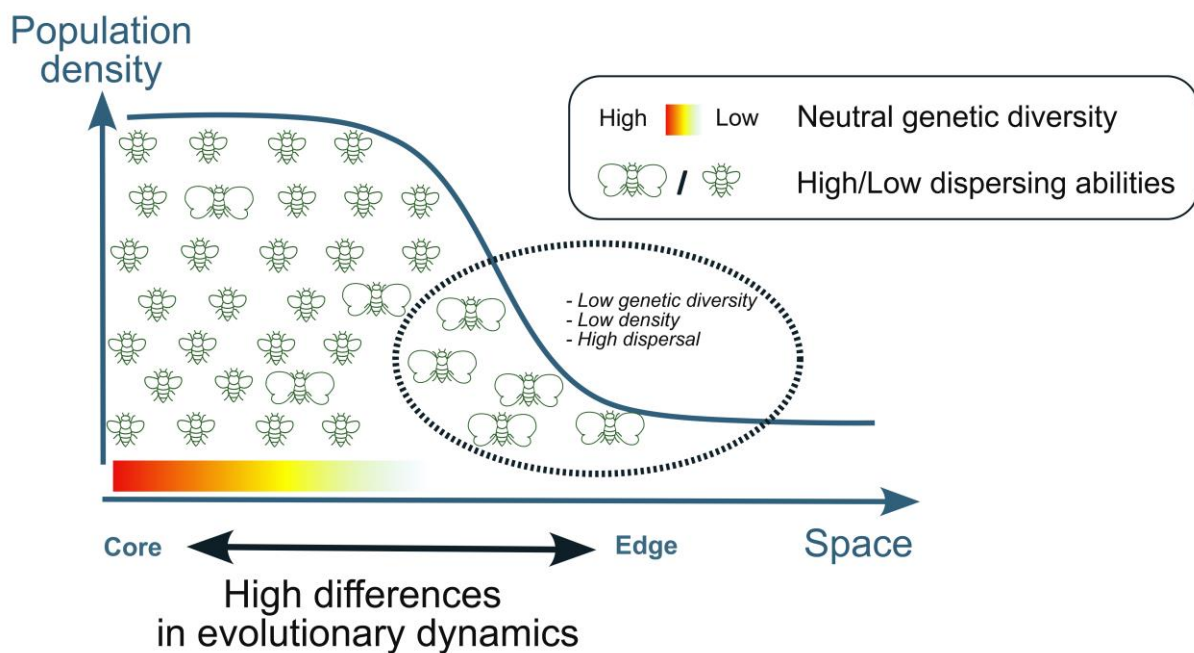


Figure I.9: Spatial sorting and natural selection within an expanding population.

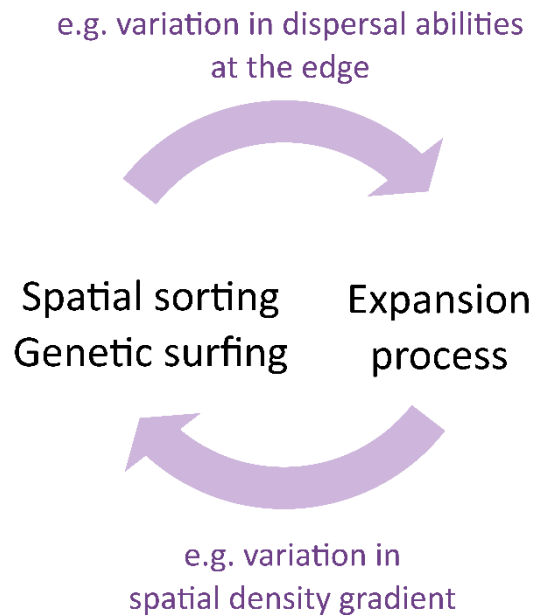
Overall, we can expect a tight interaction between the ecology of an expansion and its evolutionary processes. This is primarily because of the density gradient forming along the expansion front, which can affect both spatial and temporal evolutionary trajectories. Huge variations between high-density core populations and low-density edge ones may be observed, with edge populations presenting less neutral genetic diversity, higher dispersal abilities, as presented in [Figure I.10](#). While at first, studies focused on the eco-to-evo aspect of expansion (reviewed in Excoffier et al., 2009; Phillips et al., 2010), more and more papers started to include the feedback that evolutionary dynamics can have on ecological processes (reviewed e.g. in Miller et al., 2020) ([Figure I.11](#)). We have quickly touched on it before, with positive feedback through spatial sorting leading to good dispersers at the leading edge and accelerating expansion spread (Williams et al., 2016;



Ochocki & Miller, 2017). Fronhofer & Altermatt (2015) demonstrated, by combining experimental range expansions of *Tetrahymena* ciliates and a modelling framework, that the range expansion process led to higher dispersal, which in turn modified the density distribution within the expansion front with higher densities at the leading edge, and lower densities in the core. Negative feedback with gene surfing of deleterious variants lowers individuals' fitness at the edge, corresponding to the idea of an expansion load (Peischl et al., 2013; and Bertorelle et al., 2022 for a review on genetic load in general), and can even decelerate the spread. Peischl et al. (2015) simulated the expansion of a population with beneficial or harmful mutations on fitness within a 2-dimensional landscape: they demonstrated an accumulation of deleterious mutations, reducing fitness at the leading edge and slowing down the expansion process, with sometimes individuals from the core quickly invading the edge population if the selection is strong and far more quickly in the absence of recombination.



**Figure I.10: Expected inside dynamics of a pulled expansion**  
Modified from Vercken & Phillips (2023 in press).



**Figure I.11: Eco-evolutionary feedback loop applied to population expansions.**

Not all evolutionary (or ecological) processes are presented. Only the two most likely to highly influence the expansion dynamic compared to populations at equilibrium.

## D.2- How positive density dependence in growth and dispersal modify the inside dynamics of expansions: Pushed expansions

Previously, we saw that positive density dependence in growth or dispersal is common in nature (see [A.2](#)). Combined with what we just saw about how the internal dynamics of expansions are driven mainly by density, growth and dispersal, it is justified to assume that a modification of density-dependence on those traits will significantly influence the ecological and evolutionary processes, if this leads growth and/or dispersal to be maximal not at low densities but at higher densities behind the leading edge (Stokes, 1976).

In that case, the highest contributions to spread will not be from leading-edge individuals, but from individuals in high- or intermediate-densities located farther behind the leading edge, "pushing" forward the whole population (Stokes, 1976). In expansions presenting Allee effects, low-density populations at the leading edge may present lower or even negative growth rates in case of strong Allee effects, and it is individuals at intermediate densities that end up hypothetically contributing the most to the expansion spread (Gandhi et al., 2016). The influence on expansion dynamics can be twofold:

- First, in the presence of an Allee effect, individuals dispersing from the leading edge may not be able to establish further ahead if their density is too low, preventing the possibility to expand from this new edge after, a phenomenon also known as expansion pinning (Keitt et al., 2001). In a study on the invasive spongy moth (*Lymantria dispar*) expanding in North America, Johnson et al. (2006) demonstrated the presence of an Allee effect resulting in pulsating expansion, where the spread continues only once a small population ahead of the leading edge manages to establish by reaching a density above the Allee threshold (thanks to long-distance dispersal) and grow enough to become itself a source of enough dispersing individuals to repeat the process. The expansion profile might also become steeper as low densities under a certain threshold may not be established, and higher densities need to be reached at the leading edge before the expansion can proceed (Leung et al., 2004) (Figure I.12).
- Second, low-density populations at the edge do not present the highest growth rates, which occurs in intermediate-density populations (Figure I.2) further behind the edge. These higher growth rates at intermediate densities might lead to an increased contribution of those populations to the spread, therefore modifying the overall genetic structure and spread of the expansion. Indeed, the increased density implies that stochastic processes will have less influence on genetic diversity, and the decrease in expansion spread allows for core and front individuals to have more possibilities to mingle. It results in higher neutral genetic diversity at the edge compared to similar expansions without Allee effects (comparing Figure I.10 and Figure I.14) (Roques et al., 2012; Bonnefon et al., 2013, 2014; Gandhi et al., 2019; Foutel-Rodier & Etheridge, 2020; Birzu et al., 2021).

As for positive density-dependence in dispersal, similar assumptions on the expansion profile and genetic diversity can be made, but as a result of different causes: by having a higher dispersal rate as the density grows, it is the population more behind the leading edge that will contribute the most to expansion spread. The overall contribution of those populations will also depends on the dispersal kernel: even if high dispersal rates way behind the leading edge are high, if dispersal distance does not allow individuals from this region to reach the leading edge, then the region cannot directly contribute to the spread.

We can observe weaker successive bottleneck effects than pulled expansions by having a constant arrival of individuals coming from higher densities and lower probabilities to disperse if at low densities. Consequently, the neutral genetic diversity at the front in such expansions will decrease slower than similar expansions without positive density-dependence in dispersal (Figure I.12) (Birzu et al., 2019; Haond et al., 2021; see also Appendix 1), with weaker genetic drift therefore less stochasticity across realisations (Williams & Levine, 2018).

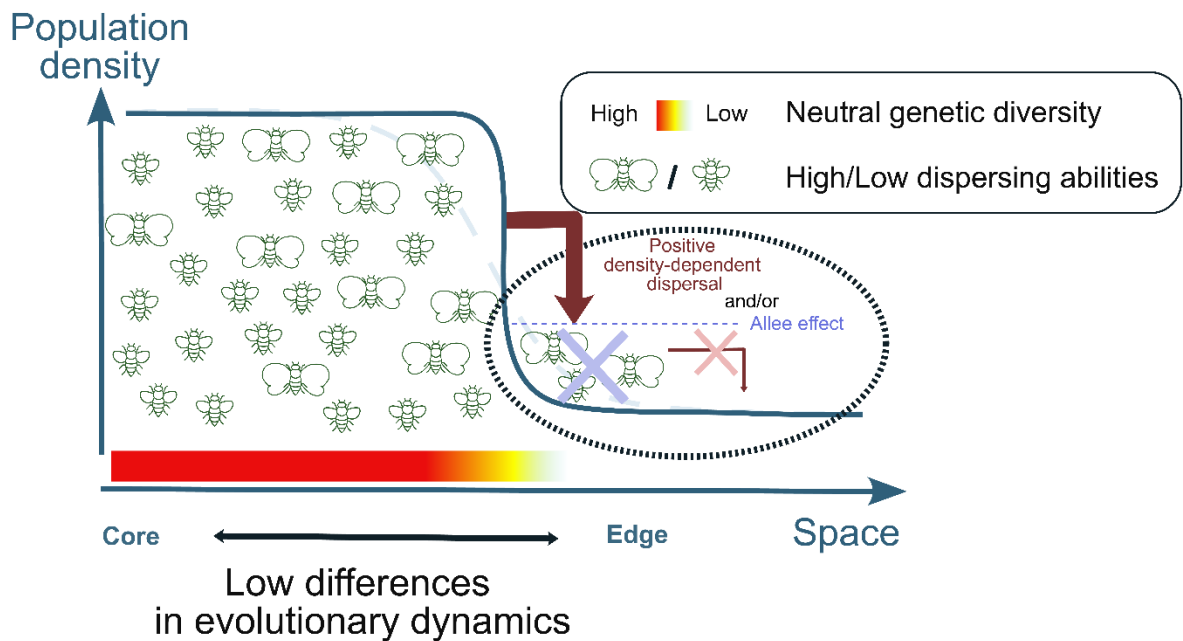


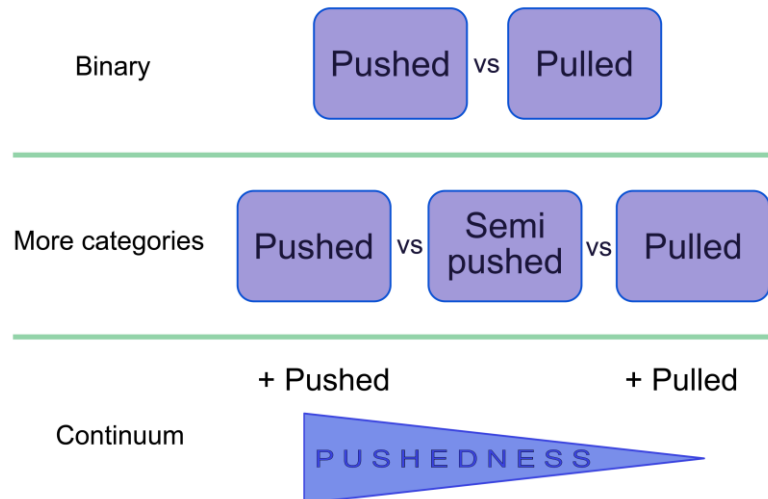
Figure I.12: Comparison of the expected inside dynamics of pushed expansion  
 Modified from Vercken & Phillips (2023 in press).

### D.3- The study of pushed/pulled expansions: from a dichotomy to an evolving continuum

In the literature, the concept of pushed and pulled expansions was originally a clear-cut dichotomous separation: expansions were either pushed or pulled, and distinct mathematical definitions and equations were used to describe the behaviour of each (Stokes, 1976; Lewis et al., 2016) (Figure I.13 top).

However, more recent works showed we can actually observe intermediate categories between pulled and pushed expansions. Birzu et al. (2018) presented the possibility of a third category they termed semi-pushed expansions (but see also Panja, 2004; Haond et al., 2021; Zhu et al., 2023) (**Figure I.13** middle). Semi-pushed expansions presented large fluctuations at the leading edge, similar to pulled dynamics, but also a higher contribution to the spread by individuals behind the edge, like pushed dynamics, taking from both pulled and pushed assumptions. It opened the door to the idea of a continuum, going from highly pulled to highly pushed expansions, mainly depending on the strength of the observed density dependence on growth or dispersal, leading to continuous variation in expansions' genetic and demographic dynamics as density dependence increases (Sullivan et al., 2017; Birzu et al., 2018; Gandhi et al., 2019; Zhu et al., 2023) (**Figure I.13** bottom).

Whether "pushedness" is a dichotomous separation or a continuum, it had been suggested that the ratio between observed expansion velocities and theoretical expectations is a strong signature of (more) pushed expansions. In practice, we could compare the actual velocity of an expansion to the theoretical velocity calculated using low-density growth and dispersal (see equation in **D.1**). Indeed, for pushed expansions, as growth and dispersal are not maximal at low densities and not the main drivers for the spread velocity, populations should expand faster than expected from that "pulled" theoretical velocity (e.g. Gandhi et al., 2019). The  $\frac{v}{v_F}$  ratio between observed and theoretical velocities can then be used or seen as a general proxy of the underlying positive density-dependence, to determine if a studied expansion is more pulled or more pushed. However, the data needed to estimate theoretical "pulled" velocities (and thus the above ratio) can be inconvenient to extract in natural populations. Indeed, the need for dispersal and/or growth data at very low densities can be challenging, especially when low-density edge populations are hard to detect or stochasticity is high. Because pushed and pulled expansions differ in so many demographic and genetic dimensions (see in **D.1** and **D.2**), we believe it may be possible to develop other indices/predictors of pushedness relying on other metrics that are easier or faster to collect. This intriguing new venue will be the subject of one part of the thesis.



**Figure I.13: Evolution of the perception of the pushed/pulled concept.**

Binary: an expansion could either be pulled or pushed. More categories: demonstrating semi-pushed expansions, e.g., Birzu et al. (2018) proposed intermediate categories. Continuum: The concept that expansions can be placed along a gradient of "pushedness", going from highly pulled expansions to highly pushedness as pushedness increases.

#### D.4- Key gaps in pushed/pulled theory linked to eco-evolutionary feedback and trait correlations

Most theoretical studies of pulled versus pushed dynamics ignore individual trait variation (e.g. Bonnefon et al., 2013, 2014; Joshi et al., 2018; Wang et al., 2019; Birzu et al., 2019, 2021). However, Allee effects and positive density-dependence in dispersal are actually underpinned by individual traits and, like any other trait, these may evolve during an expansion (Chuang & Peterson, 2016). Regarding Allee effects, Erm & Phillips (2020) were as far as we know the first to demonstrate how the evolution of the Allee effects shifted pushed expansions towards more pulled dynamics. This shift resulted from a rapid evolution toward resistance to Allee effects at the leading edge. Regarding the evolution of positive density-dependent dispersal, no paper actually tested the direct effect of dispersal traits evolution on pulled or pushed dynamics before. This question will be first explored in the article presented in [Appendix 1](#).

Another aspect that could overlay with eco-evolutionary feedback is trait correlation. As presented before, correlations could constrain the evolutionary trajectories of traits, and

we know that trait correlations influence eco-evolutionary dynamics (see [Figure 1.6](#) and the associated paragraph). The eco-evolutionary dynamics inside an expansion are also affected by trait correlations, as shown by Ochocki et al. (2020). In that study, the negative correlation between dispersal and demography constrained the positive influence of evolution on expansion spread, with strong negative correlations even resulting in a deceleration of the expansion (see also Chuang & Peterson, 2016). In the context of pushed/pulled continuum, Urquhart & Williams (2021) quickly mentioned how landscape fragmentation and a negative correlation between dispersal and fecundity altered the eco-evolutionary dynamics during expansion. They found that a patchy landscape did generate expansions with more pushed dynamics on a demographic aspect, but not for the spatial genetic structure. This finding is interesting as it opens the possibility that both trait correlation and the environmental context can potentially disconnect the demographic and genetic expectations of a pushed or pulled expansion.

## E- Presenting the goals

In this introduction, we quickly reviewed the central role of density and how traits may respond differently to varying density levels. We saw how this density dependence could influence evolutionary trajectories, which in turn influence ecological dynamics, resulting in eco-evolutionary feedback. Then, we discussed how population expansion is a particular context that can impact ecology and economics. We saw that expansions can start in various ways and that they are increasing in number. Among the numerous studies on biological expansions, the notion of pushed versus pulled is becoming mainstream, but many knowledge gaps remain in the theory and its applications. In this thesis, I will focus on three questions, each trying to fill some of these gaps. As we saw that many studies analysed pushed expansions generated by Allee effects, even though dispersal is known to be a major trait in ecology (Clobert et al., 2012; Bonte & Doherty, 2017), I decided to focus my studies on pushed expansions generated by positive density-dependence in dispersal.

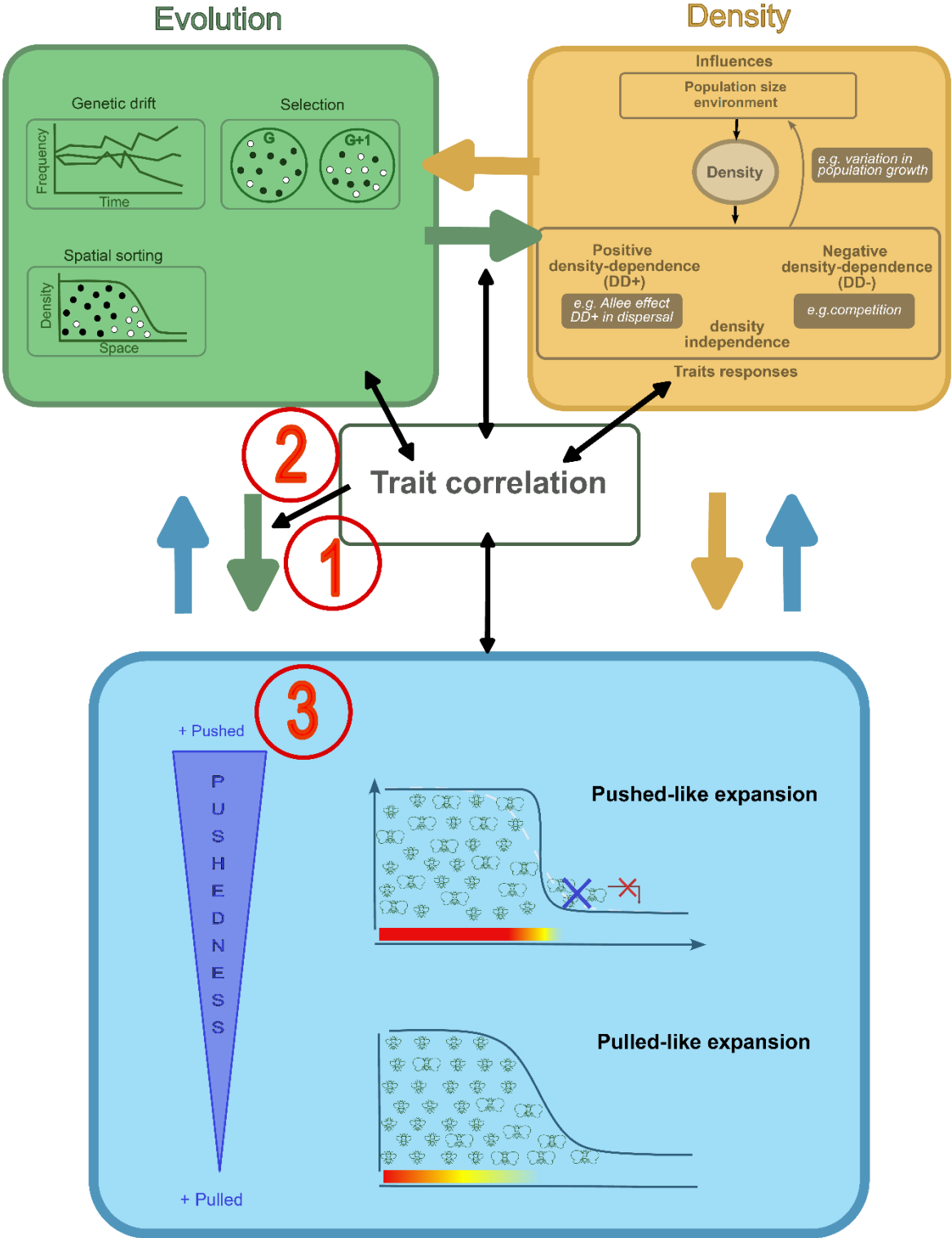
First ([Chapter II-](#)), I will examine how the interspecific position on a pace-of-life axis and its evolution can influence pushed/pulled dynamics. For this, different species of *Trichogramma* wasps with varying positions along the pace-of-life axis were studied in

experimental expansion. I will observe the evolutionary response of development time, fecundity and dispersal at different density levels alongside the demographic dynamics of each replicate (**Figure I.14**, question 1).

In the next chapter (**Chapter III-**), I will continue investigating the link between trait correlations and eco-evolutionary dynamics of pushed/pulled dynamics. Focusing this time on simulated populations, I will examine whether the evolution of a juvenile survival-adult fecundity tradeoff and dispersal traits can reshape the pushed/pulled dynamics, which in turn can influence evolutionary trajectories (**Figure I.14**, question 2).

As discussed above (**D.3**), the "true" determination of whether an existing expansion is (more or less) pushed typically relies on metrics that may be challenging or slow to obtain in natural expansions (the actual strength of the positive density dependence, or its consequences on the observed/theoretical velocity ratio). In the last chapter (**Chapter IV-**), I will try to find a set of easy-to-get metrics that could, when combined, tell us more about an expansion's pushed/pulled nature (**Figure I.14**, question 3).





Pushed/Pulled expansions

Figure I.14: Global overview of the three goals positions within the pushed/pulled and eco-evolutionary dynamics.

Please note that density (in orange) and pushed/pulled expansions (in blue) can be seen as the ecological side of the eco-evolutionary dynamics but are represented separately here.

## II- Does my pace dictate my expansion? The influence of the pace-of-life axis position on expansion dynamics in *Trichogramma*

**Article 1: Life-history traits, pace of life and dispersal among and within five species of *Trichogramma* wasps: a comparative analysis**

**Article 2: Life-history variation shapes the speed and internal dynamics of expansion in three *Trichogramma* wasp species**



## A short presentation of *Trichogramma* wasps

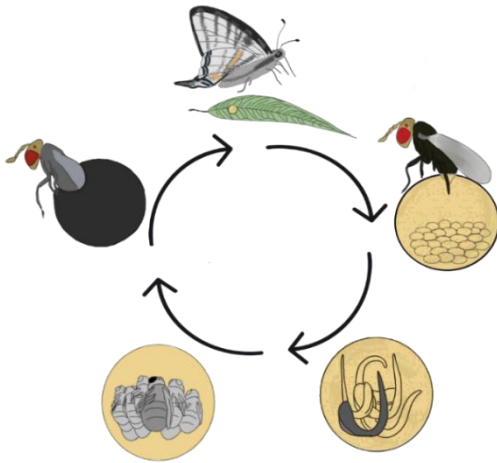


**Figure II.1:** Picture of *Trichogramma* on *Ephestia kuehniella* eggs

by Géraldine Groussier. Insert: Picture comparing a *Trichogramma* to a one-euro cents coin by Chloé Guicharnaud.

The first part of this thesis uses experimental expansions to answer how the pace of life may influence pushed/pulled dynamics. The biological models chosen for these experiments are different species of *Trichogramma* wasps. As demonstrated in previous experimental studies (Özder & Kara, 2010; Sari et al., 2021; Tabebordbar et al., 2022), *Trichogramma* wasps present many characteristics that make them excellent experimental biological models: they are small with a short life cycle, and their use as biocontrol agents means that on one hand variety of lines available to explore, and on the other hand opens the possibility of using our results later to improve *Trichogramma* biological control methods.

*Trichogramma* Westwood, 1833 (Hymenoptera: Trichogrammatidae) is a genus of microwasps with an adult size under one millimetre (**Figure II.1**), with over 200 species described (Consoli et al., 2010). They are oophagous endoparasitoids, using other insects' eggs as hosts for their eggs to develop, killing the larvae inside in the process and using it as nutrients (**Figure II.2**). As biocontrol agents, killing the pest before it can even emerge prevents the attack on cultures and limits the damages compared to other biocontrol agents preying on the emerged pest. *Trichogramma* females can lay many eggs in one host (Grenier et al., 2001). However, when *E. kuehniella* is used, the majority of the time, only one egg is laid, with one adult *Trichogramma* surviving and emerging at the end of



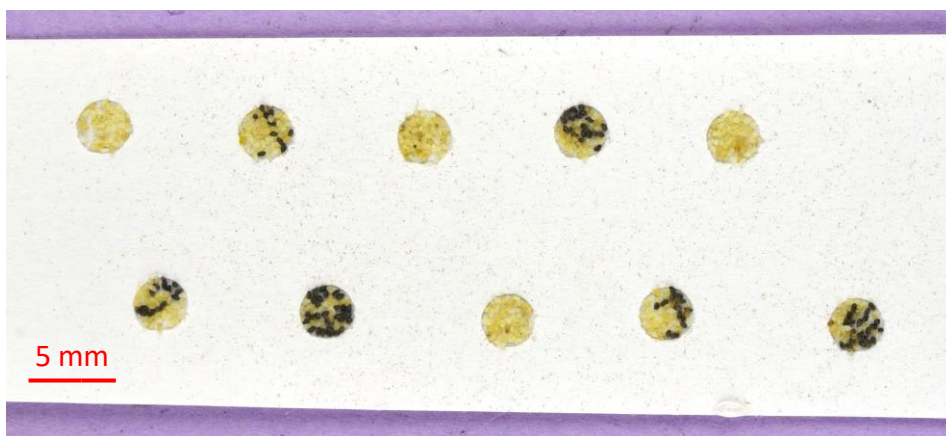
**Figure II.2: Representation of the life cycle of a *Trichogramma*.**

All pre-imaginal stages happens within the host, and only fully grown adult emerge.

Drawing credited to Alexia Cr ez e.

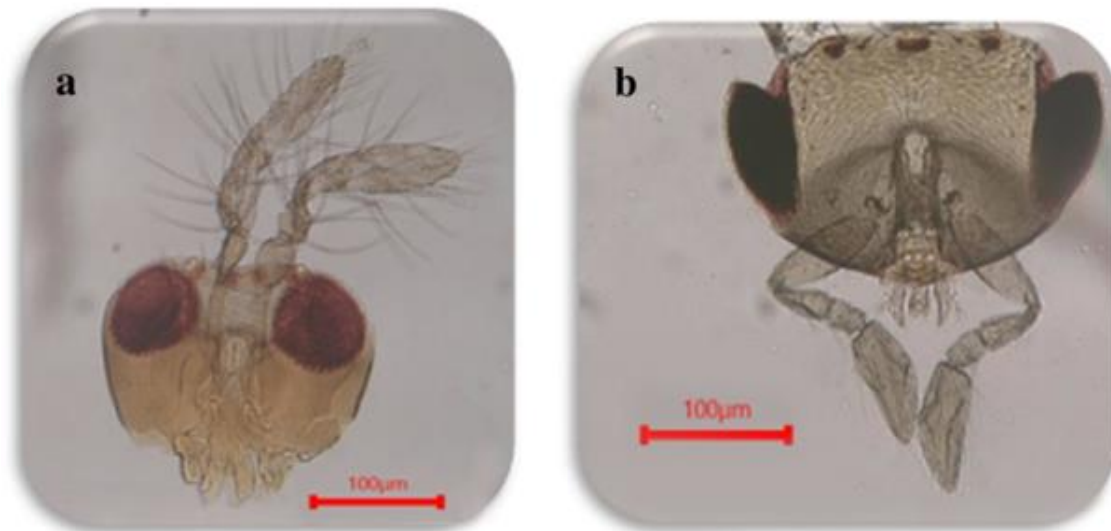
the development (Corrigan et al., 1995). It is possible to visually know when an egg is successfully parasitised about five days after parasitisation, thanks to melanin released by the developing larvae, turning the host chorion black or dark brown (Pintureau & Petinon, 1999) (Figure II.3). The combination of visual cues of infection and limited to absent superparasitism (as multiple eggs within one host) allows for easy population censuses.

*Trichogramma* are haplodiploids, with diploid females and haploid males when there are males. Indeed, while some species of *Trichogramma* are arrhenotokous (i.e. fertilised eggs develop into females while unfertilised eggs develop into males), others are thelytokous (i.e. females do not need to mate to produce diploid females) (Consoli et al., 2010). In this thesis, we only used arrhenotokous lines. In this case, it is necessary to differentiate between males and females. The easiest way to do so without killing individuals is to look at their antennae: females present clubbed antennae, while males have longer hairs (Khan et al., 2020) (Figure II.4).



**Figure II.3: A paper strip of parasitised (in black) and unparasitised (in light yellow) *E. kuehniella* eggs by *Trichogramma brassicae***

As biocontrol agents, *Trichogramma* lines are already used against many pests (most of them Lepidopteran, Smith, 1996; Zang et al., 2021). For instance, one of the species used in this chapter, *Trichogramma brassicae* (Bezdenko, 1968), is used to control lepidopteran vegetable pests such as European corn borer (*Ostrinia nubilalis*) in maize. Its protection against the pest is comparable to controls using pesticides and economically sustainable in two of the three countries studied, France and Italy (Razinger et al., 2016). While *T. brassicae* could use endangered Lepidopteran species as hosts instead of the targeted pest in Switzerland (Babendreier, Kuske, et al., 2003a), its searching efficiency in non-target habitats such as meadows resulting in low parasitism rates, lowering the risks of non-intentional effects (Babendreier, Schoch, et al., 2003; Babendreier, Kuske, et al., 2003b).



**Figure II.4:** The head capsule of a: male and b: female of one *Trichogramma* line using light micrograph; picture modified from Abdel-Galil et al. (2018).

# Article 1: Life-history traits, pace of life and dispersal among and within five species of *Trichogramma* wasps: a comparative analysis

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## Abstract

Major traits defining the life history of organisms are often not independent from each other, with most of their variation aligning along key axes such as the pace-of-life axis. We can define a pace-of-life axis structuring reproduction and development time as a continuum from less-fecund, longer-developing "slow" types to more-fecund, shorter-developing "fast" types. Such axes, along with their potential associations or syndromes with other traits such as dispersal, are however not universal; in particular, support for their presence may be taxon and taxonomic scale-dependent. Knowing about such life-history strategies may be especially important for understanding eco-evolutionary dynamics, as these trait syndromes may constrain trait variation or be correlated with other traits. To understand how life-history traits and effective dispersal covary, we measured these traits in controlled conditions for 28 lines from five species of *Trichogramma*, which are small endoparasitoid wasps frequently used as a biological model in experimental evolution but also in biocontrol against Lepidoptera pests. We found partial evidence of a pace-of-life axis at the interspecific level: species with higher fecundity also had faster development time. However, faster-developing species also were more likely to delay egg-laying, a trait that is usually interpreted as "slow". There was no support for similar covariation patterns at the within-species line level. There was limited variation in effective dispersal between species and lines, and accordingly, we did not detect any correlation between effective dispersal probability and life-history traits. We discuss how expanding our experimental design by accounting for the density-dependence of both the pace of life and dispersal might improve our understanding of those traits and how they interact with each other. Overall, our results highlight the importance of exploring covariation at the "right" taxonomic scale, or multiple taxonomic scales, to understand the (co)evolution of life-history traits. They also suggest that optimizing both reproductive and development traits to maximize the efficiency of biocontrol may be difficult in programs using only one species.

**Keywords:** dispersal syndrome; life-history strategies; fecundity; intraspecific competition; trait covariation

## Introduction

Life history describes the life cycle of an organism, how fast and how much it grows, reproduces, and survives. It is the direct product of a collection of phenotypic traits, called life-history traits (Flatt & Heyland, 2011). Those traits include growth and mortality rates, survival, reproductive investment or even the lifespan, and can be age- or stage-specific. When all life-history traits and the values they can take are combined, many pathways can lead to evolutionary success, resulting in the high diversity of what are called life-history strategies, the covariation through time and space of different traits, found across the tree of life. This high diversity can be observed at multiple taxonomic levels, from the phylum level to within species (Gaillard et al., 1989; Olsen et al., 2018; Healy et al., 2019). Yet, resource limitation means not all strategies are possible: indeed, analyses of life-history traits across taxa and hierarchical levels often reveal that a large part of the variation in organisms' life histories can be summarised on a small number of key axes, which often reflect trade-offs between life-history components. It is generally accepted that those life-history-trait correlations arise from trade-offs between allocating a certain amount of acquired resources into one trait or another, with limitations arising from a limited pool of resource to draw from, physiological constraints, and from the influence of the environment, resulting in a variety of strategies maximizing fitness (Stearns, 2000; Laskowski et al., 2021).

One specific axis has been termed the pace of life and corresponds to a correlation between life-history traits sorting organisms along a fast-slow continuum (Stearns, 1983; Braendle et al., 2011). Many trait combinations can be used to characterize a pace-of-life axis (Gaillard et al., 2016), discriminating low reproduction, long development and long lifespan (slow types) on one side from high reproduction, short development, and short lifespan (fast types) on the other. Pace-of-life axes have been identified in multiple comparative analyses across taxonomic ranks (Williams et al., 2010; Auer et al., 2018; Healy et al., 2019) although the traits that cluster to form this axis are not always the same (Bielby et al., 2007). But despite its conceptual appeal and simplicity, the pace-of-life axis should not be assumed as the one unique axis structuring life histories: the proportion of variance explained by such an axis varies between taxa (Healy et al., 2019), and in many

cases, alternative axes structuring variation also emerge (Mayhew, 2016; Bakewell et al., 2020; Wright et al., 2020). Moreover, it seems the narrower the taxonomic focus (from tree of life-wide analyses to within-species comparisons), the harder it is to find the presence of a pace of life, and the way life-history variation is structured in one species/taxon cannot always be generalized to others. Adding complexity to the correlations of life-history traits, the pace-of-life syndrome hypothesis supposes that the pace of life can co-evolve with one or many other phenotypic traits. They can be physiological (Ricklefs & Wikelski, 2002; Auer et al., 2018), behavioural (Wolf et al., 2007; Réale et al., 2010), or associated with other traits like dispersal.

Dispersal can be described as any movement potentially leading to a flux of genes or individuals across space (Ronce, 2007), and is a key component influencing both ecological and evolutionary dynamics, so much that it is sometimes described as a life-history trait in its own right (Saastamoinen et al., 2018). Dispersal often covaries with other traits, including other life-history traits (Clobert et al., 2012), in so-called dispersal syndromes (Ronce, 2012). Dispersal syndromes have been observed and compared at multiple taxonomic levels, both across (Stevens et al., 2012, 2014) and within species (Jacob et al., 2019). Therefore, it is not surprising that many works have been dedicated to the integration of dispersal along the main life-history axes, and the derivation of ecological and evolutionary implications. This includes, for instance, the idea of a trade-off between competition and colonization where species that are good at colonizing, with high fecundity or dispersal, are in return poor competitors between or among species (Yu & Wilson, 2001; e.g. Calcagno et al., 2006), and other studied links between dispersal and fecundity (Crossin et al., 2004; Gu et al., 2006; Karlsson & Johansson, 2008; Bonte & De La Peña, 2009). Rather than idiosyncratic correlations between dispersal and specific life-history traits, the pace-of-life syndrome hypothesis suggests dispersal, among others, to be a risky trait linked to the pace of life itself (Cote, Clobert, et al., 2010; Réale et al., 2010). In plants for instance, there is a relation between seed dispersal abilities and the fast-slow continuum, where a high capacity to disperse is correlated with faster life histories at the species level (Beckman et al., 2018). While many studies found a positive correlation between the pace of life and short-scale movement, like the exploration of a continuous patch, or the activity level within an arena (Rádai et al., 2017; Gangloff et al., 2017;



Lartigue et al., 2022), directly transposing short-scale conclusions like exploration or activity, to longer-scale metrics, like dispersal rates or the decision to disperse in discrete landscapes, is not always relevant (Cote, Fogarty, et al., 2010; Harrison et al., 2015; Pennekamp et al., 2019). Dispersal/life-history syndromes can lead to different ecological and evolutionary results from when traits are considered as independent. Correlation between traits, but also the strength or shape of this relationship can impact both the ecological and evolutionary dynamics of a population (Maharjan et al., 2013; Ochocki et al., 2020).

In that context, we explored first the presence of a pace-of-life axis and then the relationship between the pace of life and effective dispersal in five species of *Trichogramma* wasps. *Trichogramma* (Hymenoptera: Trichogrammatidae) are small (< 1 mm when adult) parasitoids that develop inside the eggs of their hosts, mainly Lepidoptera. They are also model species in ecology and invasion biology studies thanks to their small size, rather short development time (13-15 days, at 22 °C), or also the fact that lines can be either sexual or asexual. The goal of this study is therefore to improve our knowledge of life-history trade-offs specifically in *Trichogramma* for future studies of eco-evolutionary dynamics, but also more generally in insects, which are under-represented in both pace-of-life (but see Blackburn 1991) and pace-of-life syndromes studies (38 invertebrate species vs 141 vertebrates in Royauté et al., 2018). Potential reasons for this under-representation include a lack of data (Bakewell et al., 2020) or the difficulty to study and compare insect parasitoids, as their life-history traits are also subject to their host ecology (Mayhew, 2016). Using lab-reared lines belonging to five species of *Trichogramma*, we measured female fecundity, effective dispersal, and development time under experimental conditions, and analysed the line- and species-level covariation between these traits using multivariate Generalized Linear Mixed Models (Dingemanse & Dochtermann, 2013; Careau & Wilson, 2017). While this study is mostly exploratory, we can make some hypotheses: based on previous experiments that analysed trait variation between *Trichogramma* lines (Lartigue et al., 2022), or species (Özder & Kara, 2010), we can expect to observe trade-offs between fecundity and development time at the interline or interspecies level. In addition, as a relationship was found between activity and fecundity in Lartigue et al. (2022), there is a possibility that

one or several life-history traits are linked to effective dispersal in a dispersal syndrome at a species or line level.

## Materials and methods

### *Biological material*

*Trichogramma* are endoparasitoids, which means that females lay their eggs inside their hosts, where the larvae will develop by feeding on the host and ultimately killing it, as opposed to ectoparasitoids, who lay their eggs and develop outside their host. As some of *Trichogramma* hosts are Lepidopteran pest species, several *Trichogramma* species are used as biological control agents, and have shown to work well (Smith, 1996). For instance, *T. brassicae* is used on a large scale against *Ostrinia nubilalis*, the European corn borer (Mertz et al., 1995), and *T. evanescens*, *T. cacoeciae*, or a mix of the two species can be used against *Cydia pomonella*, an apple pest (Sigsgaard et al., 2017). In addition to their interest as laboratory model species to investigate the pace of life, the identification of correlations between life-history traits in *Trichogramma* could open up new avenues to improve their efficiency as biocontrol agents, through the optimization of their rearing or field performance (Consoli et al., 2010; Akbari et al., 2012).

For this experiment, 32 different lines of *Trichogramma* were originally selected among the collection from the Biological Resource Center (BRC) "Egg Parasitoid Collection" (CRB EP-Coll, Sophia Antipolis; Marchand et al., 2017). We restricted our choice to the only five sexual species where at least three lines were available. Within each species, we selected at random at least three lines per species and up to ten, with a total target of 32 lines for feasibility. Four lines did not correctly synchronize during preparation and could not be used, resulting in 28 lines in the actual experiment (**Table II-1**). The Biological Resource Center rears lines on eggs of the Mediterranean flour moth *Ephestia kuehniella* (Lepidoptera: Pyralidae) at 18 °C, 70 % ± 10 % relative humidity, L:D 16:8. Most lines were founded from a single original clutch each, mostly collected between 2013 and 2016 in different parts of France, and one line comes from a crossing of three single-clutch lines made in 2019 (**Supplementary Table II-1**). With approximately 15 generations per year under those rearing conditions, lines from the BRC collection are expected to have a very

low genetic variance at the time of the experiment (as seen for *Trichogramma brassicae* in the supplemental material of Dairel, Bertin, Haond, et al., 2021). Little is known about the genetic diversity in the wild, but it is expected to be low as a survey in France and Spain collected only two to three haplotypes for *T. evanescens*, *T. semblidis* and *T. brassicae* (Muru, 2021). After collecting the lines from the BRC, we kept them on *E. kuehniella* eggs at 22 °C, 70 % ± 10 % relative humidity, L:D 16:8 for two to three generations before starting the experiment. Host eggs were irradiated with UV for 15 minutes before use; this sterilization method kills the embryo while keeping it viable as a wasp host (St-Onge et al., 2014). Each female used for the experiment was isolated randomly from the rest of the population 24 hours after emerging, as *Trichogramma* start mating as soon as individuals emerge from host eggs (Doyon & Boivin, 2006). Therefore, all females during the experiment were between 24 to 48 hours old.

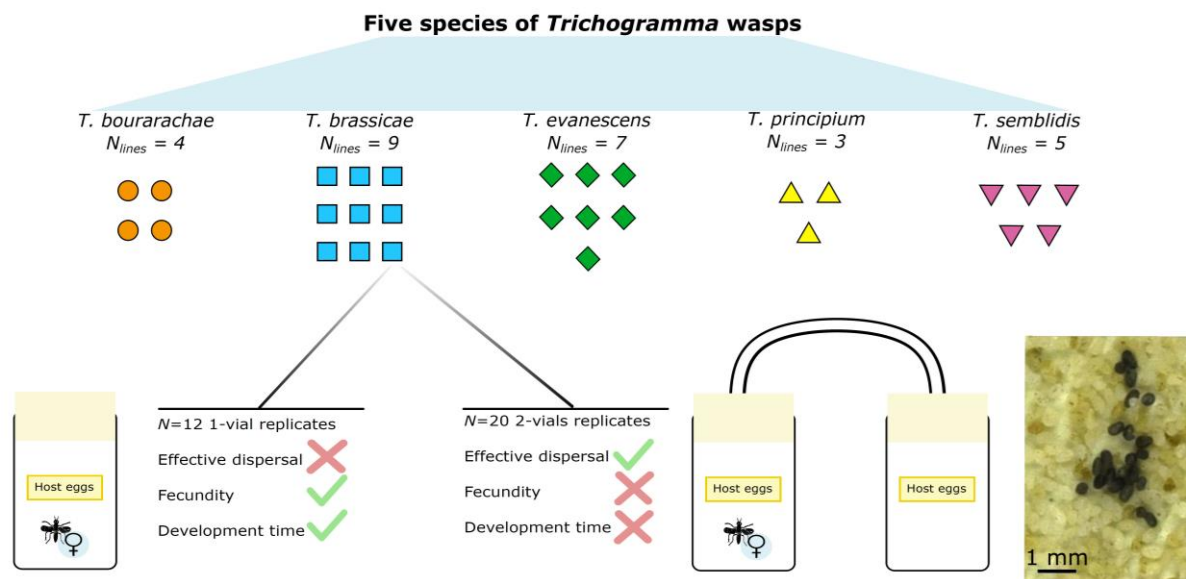
**Table II-1: Summary of the *Trichogramma* species and lines used in the experiment** among the total number of lines available in the BRC at the time.

Species	Species authority	Number of lines used (number available in the BRC)
<i>T. bourarachae</i>	Pintureau & Babault, 1988	4 (4)
<i>T. brassicae</i>	Bezdenko, 1968	9 (22)
<i>T. evanescens</i>	Westwood, 1833	7 (21)
<i>T. principium</i>	Sugonjaev & Sorokina, 1976	3 (4)
<i>T. semblidis</i>	(Aurivillius 1898)	5 (5)

### Experimental design

We used both single- and two-vial systems to measure life-history traits (**Figure II.5**). In single-vial systems (12 replicates per line), we placed one randomly selected mated *Trichogramma* female between 24 to 48 hours old into a plastic vial (5 cm diameter, 10 cm height). We also added a non-limiting quantity of irradiated *Ephesttia kuehniella* eggs on a paper strip (hundreds of host eggs in approximately 1.4 × 1 cm, see **Supplementary Figure II.1**). This system was used to measure development time and fecundity traits. In two-vial

systems (20 replicates per line), the setup was similar to the previous one, with the exception that a see-through 40 cm long plastic pipe (5 mm of internal diameter, large enough for species of less than a millimetre in size) connected the first vial (where the wasp was deposited) to another one with the same dimensions, also containing a non-limiting quantity of irradiated eggs. The ends passed through the centre of the foam plugs without protruding from them. While little is yet known about how females locate host eggs (Consoli et al., 2010), this setup was inspired by previous studies on experimental expansions on *Trichogramma* (Dahirel, Bertin, Calcagno, et al., 2021; Dahirel, Bertin, Haond, et al., 2021) and allowed us to estimate effective dispersal probability in conditions similar to previous experimental expansions. Even though fecundity and development-time data could also be collected in this second setup, we refrained from analysing them here due to the complexities of accounting for the effects of dispersal and dispersal costs, compared to the single-vial setup. Females were left in those vials for 48 h under standardized conditions: 22 °C, 70 % relative humidity, L:D 16:8. After 48 h, the egg strips were isolated in glass vials (1 cm diameter, 4 cm height), and kept under the same standardized conditions. Please note that even if plasticity can be observed in *Trichogramma* (Pinto et al., 1989; Krishnaraj, 2000), we focused our study on the presence or not of a pace-of-life under the standard conditions used in experimental expansions on *Trichogramma*, allowing us to make more direct links between our results in this study and future results in experimental expansions.



**Figure II.5: Summary of the experimental design used for measuring fecundity, effective dispersal, and development time.**

Inset (bottom right): picture of parasitized host eggs, in black, easily visible among the off-white unparasitized hosts, one week after the experiment.

### Phenotyping

For endoparasitoids, the body size is highly dependent on the host size. In our case, all species were maintained and experimented using *E. kuehniella* as host eggs, which are small enough to allow only one viable descendent (Corrigan et al., 1995) and were provided in high enough quantity to avoid superparasitism (as multiple eggs within one host might affect the viable descendent size). Therefore, we assumed that size variance was probably highly limited, with little to no correlations between hind tibia length (one proxy of individual size) and other traits (Pavlík, 1993) and did not measure size.

### Fecundity and dispersal

A week after isolation, parasitoid larvae were developed enough to blacken the host egg, allowing the visual identification of successfully parasitized eggs (picture in [Figure II.5](#)). Egg strips (one for single vial, two for two-vial systems) were then photographed (resolution: 6016 × 4016 pixels, for a real field of view size of around 12 × 8 cm) using a Nikon D750 camera (lens: AF-S Micro NIKKOR 60 mm f/2.8 G ED) fixed above the strips.

Fecundity was measured by manually counting the number of blackened eggs in each picture using ImageJ (Schneider et al., 2012). Even though superparasitism (more than one parasitoid egg laid per host) is frequent for *Trichogramma*, it tends to be avoided when an unlimited number of unparasitized eggs are present for single females (in *T. chilonis*, Wang et al., 2016). As in Özder & Kara (2010), the mean fecundity in *Trichogramma* on *E. kuehniella* was at best around a hundred, and each of our host egg strips counted several hundreds of eggs, we can assume that our study was indeed done in a non-limiting context. Furthermore, in general, only one adult emerges from *E. kuehniella* eggs in the end (Klomp & Teerink, 1966; Corrigan et al., 1995).

Egg retention by refusing to oviposit was previously observed in *T. principium* and *T. brassicae* (Fleury & Boulétreau, 1993; Reznik et al., 1998, 2001). Therefore, egg retention may be present in all of the studied species and may affect fecundity measures in the timeframe of our experiment; see below for how this possibility was accounted for in the context of data analyses.

In two-vial systems, effective dispersal (i.e. movement between patches leading to actual gene flow) was measured as a binary response, where one female is considered to have successfully dispersed if at least one parasitized egg was found on the strip present in the second plastic vial.

#### Development time

After taking the pictures for fecundity, each isolated host egg strip was checked every day at around 9:00 a.m., 12:00 p.m., and 4:00 p.m. for the presence of emerged individuals. The development time of one replicate was considered to be the number of days between the female in the plastic vial starting to lay eggs and the emergence of the first offspring. Note that the true time is only known to a precision of two days, because of uncertainty in when precisely eggs were laid during the 48 h window after introduction in the system (see Data analyses for how this is accounted for).

### Data analyses

Data were then analysed with Bayesian multivariate multilevel/mixed models, using the *brms* R package, version 2.17.0 (Bürkner, 2017a), a front-end for the Stan language (Stan Development Team, 2022). The code was tested on R versions 4.1.2 to 4.2.0 (R Core Team, 2021).

The multivariate model architecture was made of four connected Generalized Linear Mixed sub-models, one for each response that are effective dispersal, development time, and fecundity divided into two components:

- Effective dispersal (the probability that the female successfully laid eggs in the arrival patch) was modelled with a Bernoulli distribution (with a logit link).
- Development time was modelled with a Log-Normal distribution, often chosen for time-to-event data. Because of the 48 h time period where the female was allowed to reproduce, development times were interval censored (with 48 h wide intervals);
- For fecundity, initial models showed evidence of both potential zero inflation and overdispersion, therefore a Zero-inflated Negative binomial distribution was used. This effectively separates the response variable into two components, "structural zeroes" and counts, each with a valid biological meaning (Blasco-Moreno et al., 2019):
  - On one hand, the zero-inflated part of the distribution, similar to a Bernoulli model, modelled an excess of non-parasitized replicates compared to a negative binomial model. Given that egg retention is common in *Trichogramma* species, leading to delays in egg-laying of up to several days commonly (Reznik et al., 2001), a biologically plausible reading of these structural zeroes component is the probability of retention in the 48 h of the experiment;
  - On the other hand, a Negative binomial component (with a log link) was interpreted as the fecundity of individuals that did not perform egg retention. From now on, we will use "fecundity without retention" to refer to this fecundity component (i.e. the effectively egg-laying individuals

only), and "overall fecundity" will refer to the mean number of eggs laid by all individuals, including those potentially doing retention.

We used the model architecture described above for two multivariate models. The two multivariate models were fitted to observe how variance in traits and the covariance between traits are partitioned at the inter- and intra-specific levels. The first model incorporated both line and species-level effects, structuring the variance into intra- and inter-specific levels. The second model only had line effects as predictors, and therefore assumed that individuals from two conspecific lines do not resemble each other more than individuals from two randomly selected lines. In both cases, the same predictors were used for all four responses.

The first model included species-level effects as a fixed effect, mostly due to the low number of species studied, and line identity was coded as a random effect, while the second model only included line-level random effects. To account for line-level correlations between the response variables, line-level random effects for the two models were modelled as drawn from a shared variance-covariance matrix (Bürkner, 2017b).

While phylogenetic comparative methods could be used in this context, as some of the variations could be explained by shared ancestry (Felsenstein, 1985), there is no phylogenetic tree available for all lines used we could include (Hadfield & Nakagawa, 2010). Our first model, splitting variation into species and line components is nonetheless similar to the "taxonomic model" suggested in these cases where tree data are absent (Hadfield & Nakagawa, 2010).

The model formulas and the priors used (mostly weakly informative priors based on or modified from McElreath, 2020) are described in detail in Supplementary Material S3. The models were run with four chains during 4500 iterations each, with the first 2000 iterations for each chain used as warmup. This led to good chain convergence and sample size, as checked using the statistics proposed by Vehtari et al (2021). Model outputs were then checked using posterior predictive checks to compare predictions with empirical dataset (as suggested by Gabry et al., 2019). See the "Data and code availability" section for links to an archived version of the annotated model code.



## Results

*Trichogramma bourarachae* had lower fecundity without retention and higher development time than *Trichogramma brassicae*, while *T. semblidis* only had a lower development time than *T. bourarachae* but no clear difference in fecundity without retention (Table II-2, Figure II.6 B, C). There were no other clear species differences (based on 95 % intervals of pairwise differences) in fecundity or development time. We did not find any evidence for between-species differences in effective dispersal probabilities (Table II-2, Figure II.6 A). *T. brassicae* and *T. semblidis* both had higher egg retention probabilities than *T. bourarachae* (pairwise differences of 0.20 [0.00; 0.40] and 0.29 [0.05; 0.53] respectively, Figure II.6 D).

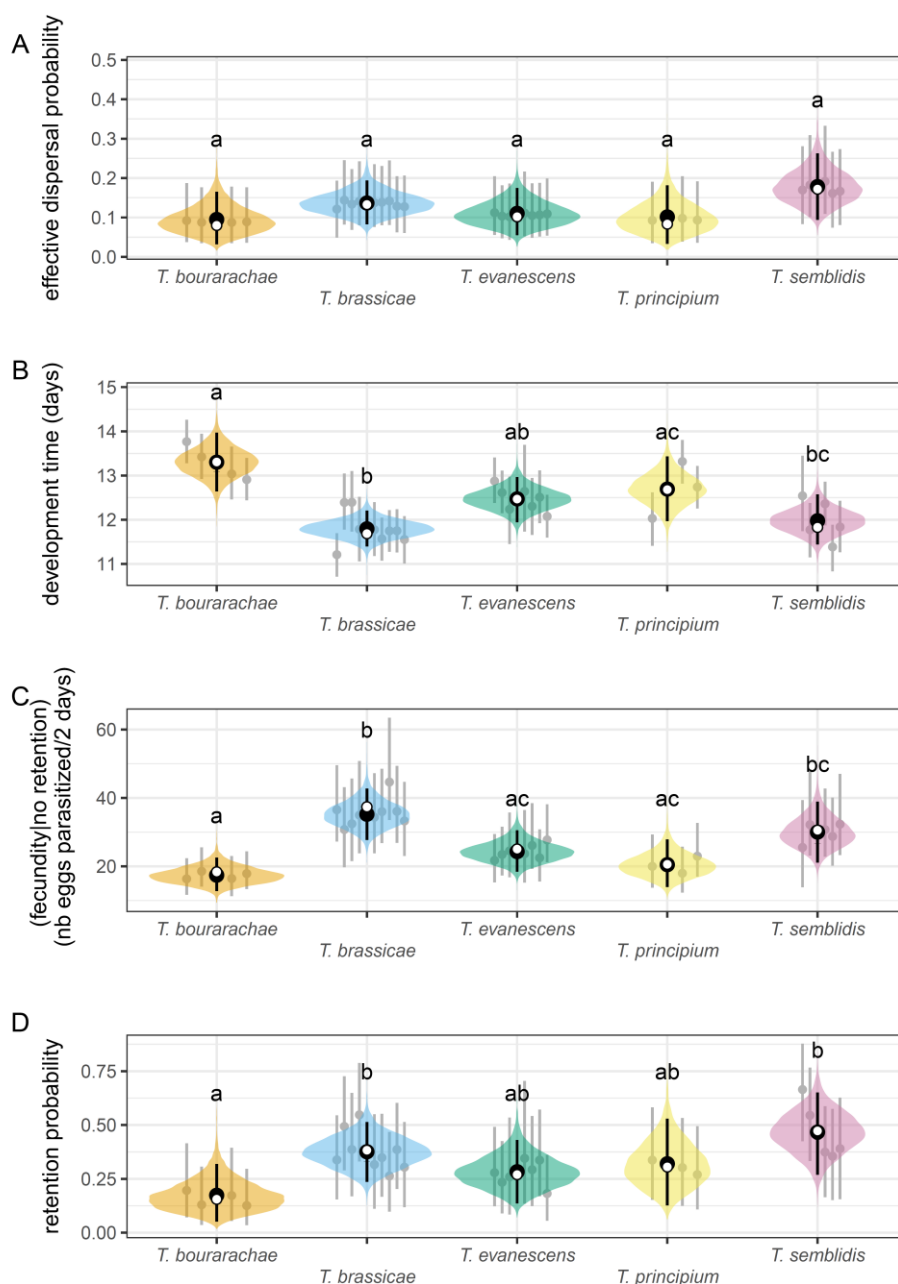
**Table II-2: Mean posterior values and 95 % posterior highest density intervals per species.**

For single female fecundity in the absence of egg retention, said egg retention probability to occur during the experiment, the development time of the first offspring and effective dispersal probability. For a given trait, two species with no index letters in common are considered to have "significant" pairwise comparison differences.

	<i>T. bourarachae</i>	<i>T. brassicae</i>	<i>T. evanescens</i>	<i>T. principium</i>	<i>T. semblidis</i>
Effective dispersal probability	0.09 <sup>a</sup> [0.03; 0.16]	0.14 <sup>a</sup> [0.08; 0.19]	0.11 <sup>a</sup> [0.05 ; 0.17]	0.1 <sup>a</sup> [0.03; 0.18]	0.18 <sup>a</sup> [0.1; 0.27]
Development time	13.3 <sup>a</sup> [12.64; 13.97]	11.79 <sup>b</sup> [11.4; 12.2]	12.47 <sup>ab</sup> [11.94; 12.96]	12.69 <sup>ac</sup> [11.95; 13.42]	11.97 <sup>bc</sup> [11.39; 12.52]
(Fecundity no retention)	17.42 <sup>a</sup> [12.77; 22.5]	35.24 <sup>b</sup> [27.71 ; 42.7]	24.31 <sup>ac</sup> [18.43 ; 30.49]	20.49 <sup>ac</sup> [13.83 ; 27.71]	30.02 <sup>bc</sup> [21.42 ; 39.2]
Retention probability	0.17 <sup>a</sup> [0.05 ; 0.32]	0.38 <sup>b</sup> [0.24; 0.51]	0.28 <sup>ab</sup> [0.14; 0.43]	0.32 <sup>ab</sup> [0.13; 0.53]	0.47 <sup>b</sup> [0.27; 0.65]

Correlations between traits at the line level were analysed through the random effect correlation/covariance matrix. In the first model, differences across species were modelled with a fixed effect, so they were not included in random effect correlations, while the second model included both species- and line-level random effects. Therefore, any qualitative difference between the two models can be interpreted as an effect at the species level.

The only detectable correlations among traits were between fecundity without retention and development time (**Table II-3**, **Figure II.7**). There was a negative correlation between these two traits at the line level in the model where species effects were not partitioned out (-0.62 [-0.92; -0.28], see **Table II-3** bottom, see also the overall pattern **Figure II.7**). However, when looking at the model where species differences are partitioned out into fixed effects (**Table II-3** top), this random effect negative correlation mostly vanishes (-0.22 [-0.76; 0.38]). This reflects the fact that the overall correlation highlighted in **Table II-3** top is mostly driven by between-species differences in both fecundity and development time (see **Figure II.6** and species averages in **Figure II.7**).



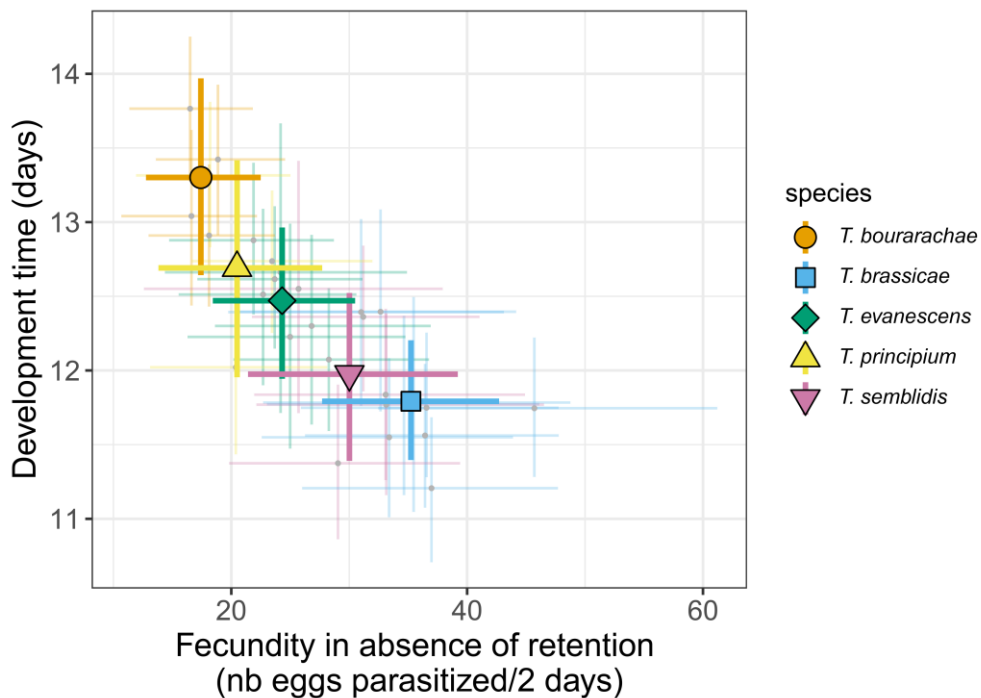
**Figure II.6: Posterior values as a function of the *Trichogramma* species.**

A) the probability of effective dispersal, B) the development time in days of the first offspring, C) the number of parasitized eggs for a single female when no retention occurred, and D) the probability for a female to perform egg retention during the experiment. 95 % posterior highest density intervals per line for each species are displayed in grey. Black dots represent posterior means and bars the 95 % intervals, while the posterior density distributions of fixed (species) effect predicted means are coloured depending on the species. For a given trait, two species with no index letters in common are considered to have "significant" pairwise comparison differences (i.e. the 95 % highest density interval of the difference does not include 0). White dots represent observed means per species, presented for illustrative purposes only (as they are calculated assuming all observed zeroes in egg numbers were attributable to retention, and using the midpoint of the 48 h interval for development time).

**Table II-3: Line-level random effect correlations among measured traits, represented by means and 95 % higher posterior density intervals.**

(top) Between-lines trait correlations, from the partitioned covariance model (species differences are excluded as fixed effects); (bottom) between-lines trait correlations from the model without fixed species effects. Intervals without 0 inside are presented in bold.

	Effective dispersal probability	(Fecundity no retention)	Retention probability
Within-species, among-line correlations (after excluding between-species differences as fixed effects)			
(Fecundity   no retention)	0.04 [-0.66; 0.72]		
Retention probability	0.04 [-0.65; 0.73]	-0.22 [-0.85; 0.4]	
Development time	0.12 [-0.58; 0.79]	-0.22 [-0.76; 0.38]	0.2 [-0.37; 0.71]
Overall among-line correlations, inclusive of between-species differences			
(Fecundity   no retention)	0.19 [-0.46; 0.82]		
Retention probability	0.15 [-0.52; 0.81]	0.08 [-0.48; 0.61]	
Development time	-0.08 [-0.71; 0.59]	-0.62 [-0.92; -0.28]	-0.17 [-0.64; 0.31]



**Figure II.7: Posterior development time of *Trichogramma* species as a function of posterior fecundity in the absence of egg retention.**

Coloured crosses represent species 95 % posterior higher posterior density intervals for development time and fecundity, while coloured symbols represent species posterior means; line-level posterior means are displayed in grey and line-level posterior 95 % intervals are displayed in the colour of their corresponding species but more transparent.

## Discussion

### *Identification of one interspecific Pace-of-Life axis in Trichogramma*

We found a negative between-line correlation between development time and fecundity in this subset of five *Trichogramma* species, with high fecundity without retention, fast development time on one side, and low fecundity, slow development on the other (**Figure II.7, II.6, Table II-3**). This correlation, which matches the classical pace-of-life axis (Healy et al., 2019) is mainly or only due to species-level differences: species with higher fecundity also had faster development times (**Figure II.7, II.6**), and the line-level correlation vanishes when species differences are partitioned out (**Table II-3**). We note that even if there is no statistically significant correlation when the variance is structured within species and among lines, the sign of this correlation remains negative (**Table II-3 top**), following a similar tendency to the interspecific negative correlation observed in **Table II-3 bottom**. Having relatively similar patterns of interspecific and intraspecific correlation may result from close genetic correlations between development time and fecundity in *Trichogramma*, through pleiotropy or other strong genetic architecture, constraining the evolution of this trade-off among lines and species (Peiman & Robinson, 2017). It is also possible that at the metabolic level, resource acquisition and allocation may favour longer development times at the expense of fecundity or the opposite (Stearns, 2000; Jørgensen & Fiksen, 2006; Agrawal, 2020). The fact that a pace of life was found at the between-species level but not conclusively at the within-species level is in line with the existing literature, in which consistent pace-of-life axes are considered increasingly difficult to find as the taxonomic level narrows down, possibly due to scale-dependent mechanisms (Simons, 2002; Agrawal, 2020). Correlations at the species level act over a longer macroevolutionary timescale, where divergent positions on the pace-of-life axis of each species may represent long-term trade-offs and selection pressure over a wider environmental range than at lower levels, like lines. For lower levels, such as lines or individuals, traits may be more responsive to direct environment variation through phenotypic plasticity, and a shorter evolutionary timescale may lead to lower variation range compared to a higher level (Siefert et al., 2015).

However, this pace-of-life finding is based on splitting fecundity into what we interpret as egg retention and fecundity without retention components. While a significant negative correlation with development was found on the latter component of overall fecundity, results are more complex for retention probabilities. Indeed, there is no evidence for the line-level correlation between egg retention and other life-history traits (**Table II-3**). Furthermore, at the species level, faster species (lower development time and higher fecundity in the absence of retention) were also the species with the highest retention probabilities (**Figure II.6, Table II-2**). If we interpret retention rates as a trade-off between present reproduction and future opportunities, then high retention can be seen as a "slow" trait; its association with "faster" life history traits may then appear paradoxical. It might be that fecundity in the absence of retention and retention probabilities are not actually separate traits, and that the trait correlations described above derive from their "artificial" separation by the statistical model. However, previous studies indicate that in *T. principium*, except for prolonged periods of egg-retention, individuals manifesting egg retention had similar fecundities in their first days of actual egg-laying and similar lifetime fecundities than individuals that did not (Reznik et al., 1998, 2001). Still in *T. principium*, there are indications that individuals manifesting egg retention have longer mean lifespans than individuals that immediately oviposit (Reznik et al., 2003; Reznik & Vaghina, 2007). These results support the idea that egg retention is a separate trait, interpretable as a mark of delayed reproduction (thus typically "slow" life history) rather than merely a component of reduced reproduction. While the pace of life remains an important and valuable structuring pattern in life histories, our results would agree with other studies showing that deviations from naïve expectations, where all traits should be either "slow" or "fast", can be frequent (Bielby et al., 2007; Wright et al., 2020). In Wright et al (2020), their eco-evolutionary model presented possibly unexpected but existing life-history strategies, like "slow" adult reproduction alongside "fast" offspring survival (that the authors likened to an oak tree life history) or the opposite (represented by mayflies). However, because egg-laying was restricted to a 48 h window in our experiment, we cannot yet confirm this interpretation. Further studies measuring lifetime reproductive success, longevity or the way reproductive effort is spread throughout the lifetime may shed more light on the way life history is structured in *Trichogramma* wasps.

*No evidence for a syndrome linking effective dispersal probability and the pace of life*

Effective dispersal probability varied the least among the four traits measured, with no evidence of between-species or even between-lines differences (**Figure II.6**), and values were rather consistent with previous studies (Dahirel, Bertin, Calcagno, et al., 2021). There was also no correlation between effective dispersal and any of the other traits (**Table II-3**), meaning that there is no evidence for dispersal/life-history syndromes at the line or species level in our set of *Trichogramma* species. Interestingly, this result on effective dispersal between patches completes previous studies on the activity of *Trichogramma* species. In Wajnberg & Colazza (1998), the authors showed a significant difference in the average area searched within one patch by *T. brassicae* isofemale lines while our results showed no differences in effective dispersal (**Figure II.6**). In Reznik & Klyueva (2006), *T. principium* females manifesting egg retention had higher dispersal activity in a continuous environment than females that laid eggs beforehand. This discrepancy may be the result of a focus on different taxonomic levels: Reznik and Klyueva (2006)'s results deal with within-species and within-line covariation, versus between-lines and between-species in the present study. It may also result from differences in experimental designs and metrics used: the dispersal metrics used in Reznik and Klyueva (2006) are based on short-term (less than one day) and short-distance (up to 5 cm) movement on a continuous arena, compared to our experiment (two days and 40 cm between discrete patches). In that case, there may still exist in *Trichogramma* a pace-of-life syndrome linking life history to short-term activity and behaviour, but not effective dispersal. Indeed, correlations between short-term movement activity and life-history traits were also found in *T. evanescens* at the between-line level (Lartigue et al., 2022). While short-term activity metrics in uniform continuous environments are often considered valid proxies of longer-term dispersal between discontinuous patches (Pennekamp et al., 2019), this comparison of our study with the existing literature shows that this is not always the case. Dispersal is extremely context-dependent, including current resource availability (Fronhofer et al., 2018); there is furthermore evidence that correlations between dispersal and other traits can be altered depending on whether individuals disperse from high-resource or low-resource contexts (Cote et al., 2022), but also how density can have an impact on both

dispersal behaviour and its evolution (Poethke & Hovestadt, 2002; Clobert et al., 2009; Bitume et al., 2013; Poethke et al., 2016).

#### *The potential implications of context-dependence and especially density-dependence*

Building on this point, our study ignored this potential for context dependence, as every female tested for a given trait was tested under the same low-density conditions (alone in the experimental design with a non-limiting host supply). Dispersal syndromes (Ronce, 2012; Bonte & Doherty, 2017; Cote et al., 2022) and also pace-of-life syndromes can be context-dependent. Behavioural types can be dependent of the dispersal status and predation risks (Bell & Sih, 2007; Cote, Clobert, et al., 2010). Pace-of-life syndromes and/or their constituent traits may also depend on resource acquisition through plastic responses (Montiglio et al., 2018; Laskowski et al., 2021) or quality. In *Trichogramma* for instance, host egg species and quality can influence life-history traits (Paul et al., 1981), and we used a substitution host in the present study. Recent works suggest that population density and density fluctuations, in particular, may also play a key role in shaping the presence of a pace of life in the first place (Wright et al., 2020) and its association with behaviours: fast individuals may have a higher reproductive rate in low-density contexts, but their lower intra-specific competition is a disadvantage when close to the carrying capacity of an environment, and therefore are more likely to disperse to escape to lower densities where this competition is lessened (Wright et al., 2019). This interaction between the pace of life and density may interact with the overall density dependence of dispersal (Clobert et al., 2009; Harman et al., 2020), altering syndromes linking dispersal and life history. Given that there is evidence for dispersal and/or fecundity being density-dependent in several *Trichogramma* species (*Trichogramma achaeae*, *T. chilonis* and *T. euproctidis*, Zboralski et al., 2016; *T. brassicae*; Dahirel, Bertin, Calcagno, et al., 2021), further studies including density dependence may lead to more generalizable insights about pace of life and dispersal in *Trichogramma*.

#### *Implications for biocontrol improvement and perspectives*

While studies on trade-offs (Bennett et al., 2002; Reznik & Klyueva, 2006; Zboralski et al., 2016) or pace-of-life syndromes (Lartigue et al., 2022) already existed in small biocontrol agents including *Trichogramma*, our results provide new insights on between-species



comparisons and the taxonomic scales at which trait variation is important. Some species like *T. evanescens*, *T. cacoeciae* (Sigsgaard et al., 2017) or *T. brassicae* (Özder & Kara, 2010) are already well used as biocontrol agents. In that context, a choice might be needed between maximizing one trait or a set of traits of interest at the expense of the others. For *Trichogramma*, while having fast-developing and high-fecundity individuals can be beneficial to quick intervention and a higher number of host eggs parasitized, they are reared and released mainly at high densities, (Consoli et al., 2010) densities for which individuals with longer development time might fare better against the intra-species competition (Wright et al., 2019). For inoculative releases, where a small population of biocontrol agents in the area of interest must establish itself and reach higher densities in further generations, both fecundity and competitive abilities are to be favoured for efficiency (Smith, 1996). Our results suggest that for some purposes, selecting different species might actually be more successful than attempting to select specific lines within one already used species.

## Data availability

Data and R code to reproduce all analyses presented in this manuscript are available on GitHub ([https://github.com/CGuicharnaud/Trichogramma\\_POL\\_dispersal\\_2023](https://github.com/CGuicharnaud/Trichogramma_POL_dispersal_2023)) and archived in Zenodo (<https://doi.org/10.5281/zenodo.7544901>).

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## Author contributions

CG, GG, EV and MD designed the experiment. Lines rearing was done by LL and CG, while CG, GG, EB, LL and EV conducted the experiments in the lab. CG and LL collected data; CG and MD analysed the data. CG wrote the first draft; all authors were able to read, edit, and approve the manuscript.

## Conflict of interest disclosure

The authors declare that they comply with the PCI rule of having no financial conflicts of interest in relation to the content of the article. The authors declare the following non-financial conflict of interest: EV is a recommender of several PCI (PCI Evolutionary Biology, PCI Ecology and PCI Zoology)

# Article 1: Supplementary Materials

## Supplementary Material 1 - Detailed information for lines used

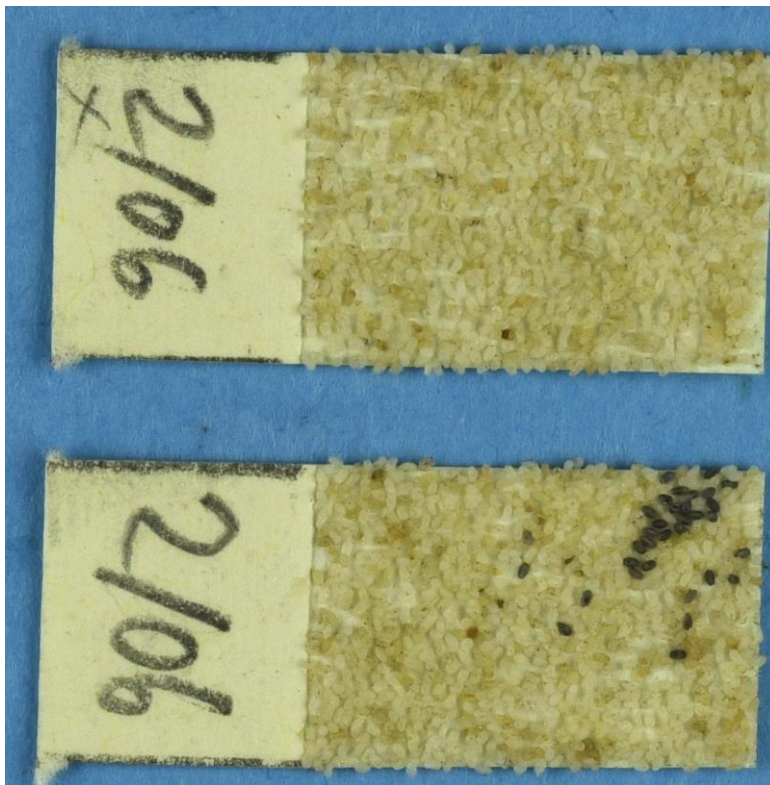
**Supplementary Table II-1: Detailed information on the lines used**

with the country, department, GPS coordinates of collection place and the date when samples were collected. Lines marked with a \* were shared by the biocontrol firm BioLine as part of a collaborative project (<https://www.colbics.eu/Main-Results/Intraspecific-diversity-in-Trichogramma-brassicae>), but their precise geographic origin is kept confidential

Species	Lines	Capture year	Country	longitude	latitude
<i>T. bourarachae</i>	ISA11967	2016	France	6.90	43.82
<i>T. bourarachae</i>	ISA11969	2016	France	6.90	43.82
<i>T. bourarachae</i>	ISA5544	2015	France	7.12	43.65
<i>T. bourarachae</i>	ISA6646	2015	France	6.90	43.82
<i>T. brassicae</i>	F5-8*	2013	France	-	-
<i>T. brassicae</i>	F3-2*	2013	France	-	-
<i>T. brassicae</i>	F3-9*	2013	France	-	-
<i>T. brassicae</i>	F5-11*	2013	France	-	-
<i>T. brassicae</i>	F5-12*	2013	France	-	-
<i>T. brassicae</i>	F6-4*	2013	France	-	-
<i>T. brassicae</i>	I2-16*	2013	Europe	-	-
<i>T. brassicae</i>	I6-5*	2013	Europe	-	-
<i>T. brassicae</i>	PR002	2015	France	5.43	43.59
<i>T. evanescens</i>	BIO-XK	2013	France	4.38	44.53
<i>T. evanescens</i>	BIO-XE	2013	France	6.88	43.59
<i>T. evanescens</i>	BIO-XA	2010	France	6.11	43.9
<i>T. evanescens</i>	N-05	2016	France	-0.78	43.49
<i>T. evanescens</i>	Q-05	2015	France	3.58	45.67
<i>T. evanescens</i>	HY-05	crossing of three lines from Lartigue et al. (2022) made in 2019			
<i>T. evanescens</i>	H-03	2016	France	4.93	44.98
<i>T. principium</i>	81a	1975	France	6.13	43.12
<i>T. principium</i>	ISA11235	2016	France	7.18	43.77
<i>T. principium</i>	ISA11367	2016	France	7.19	43.74

Species	Lines	Capture year	Country	longitude	latitude
<i>T. semblidis</i>	FPV025	2015	France	4.88	45.95
<i>T. semblidis</i>	PR007	2015	France	5.43	43.59
<i>T. semblidis</i>	CVR065	2016	France	0.44	44.21
<i>T. semblidis</i>	FPV034_A	2015	France	4.88	45.95
<i>T. semblidis</i>	BL110	2016	France	0.89	45.2

## Supplementary Material 2 - Picture of the experimental design



**Supplementary Figure II.1: Picture of host eggs strips used in a two-vial system.**

Parasitized host eggs are identified by their blackened state compared to unparasitized host eggs.

## Supplementary Material 3 - Detailed description of statistical models

The development times  $T_{s,l,i}$ , overall fecundities  $F_{s,l,j}$  and effective dispersal probabilities  $D_{s,l,k}$  for each observation  $i, j$  or  $k$  from each line  $l$  belonging to species  $s$  can be modeled using the following multivariate model (note that due to interval censoring,  $T_{s,l,i}$  is not observed directly, only a 2-day wide interval  $[t_{s,l,i}; t_{s,l,i} + 2]$  such that  $t_{s,l,i} \leq T_{s,l,i} \leq t_{s,l,i} + 2$ ):

$$T_{s,l,i} \sim \text{Log Normal}(\mu_{s,l}, \sigma_{[T]}),$$

$$F_{s,l,j} \sim \text{ZINegative-Binomial}(\pi_{s,l}, \lambda_{s,l}, \varphi),$$

$$D_{s,l,k} \sim \text{Bernoulli}(p_{s,l}),$$

Where  $\pi$  is the probability of excess zeroes, which we interpret in this context as the retention probability.

*Model partitioning variance between species fixed effects and lines random effects*

The models for each parameter are then as follows:

$$\mu_{s,l} = \beta_{[\mu]s} + \alpha_{[\mu]l},$$

$$\text{logit}(\pi_{s,l}) = \beta_{[\pi]s} + \alpha_{[\pi]l},$$

$$\log(\lambda_{s,l}) = \beta_{[\lambda]s} + \alpha_{[\lambda]l},$$

$$\text{logit}(p_{s,l}) = \beta_{[p]s} + \alpha_{[p]l},$$

The line-level random effects are distributed as follows:

$$\begin{bmatrix} \alpha_{[\mu]l} \\ \alpha_{[\pi]l} \\ \alpha_{[\lambda]l} \\ \alpha_{[p]l} \end{bmatrix} \sim \text{MVNormal} \left( \begin{bmatrix} 0 \\ 0 \\ 0 \\ 0 \end{bmatrix}, \Omega \right)$$

Where the line-level covariance matrix  $\Omega$  can be decomposed into the random effects standard deviations and the correlation matrix  $R$ :

$$\Omega = \begin{bmatrix} \sigma\alpha_{[\mu]} & 0 & 0 & 0 \\ 0 & \sigma\alpha_{[\pi]} & 0 & 0 \\ 0 & 0 & \sigma\alpha_{[\lambda]} & 0 \\ 0 & 0 & 0 & \sigma\alpha_{[p]} \end{bmatrix} R \begin{bmatrix} \sigma\alpha_{[\mu]} & 0 & 0 & 0 \\ 0 & \sigma\alpha_{[\pi]} & 0 & 0 \\ 0 & 0 & \sigma\alpha_{[\lambda]} & 0 \\ 0 & 0 & 0 & \sigma\alpha_{[p]} \end{bmatrix}$$

We set weakly informative priors as suggested in McElreath (2020). We used a Normal ( $\log(11)$ , 1) and Normal ( $\log(19)$ , 1) prior for fixed effect species intercepts  $\beta_{[\mu]}$  and  $\beta_{[\lambda]}$  respectively. The prior means here were shifted from the usual 0 to values based on the mean development time and fecundity of *Trichogramma* in our dataset. We used

Normal(0, 1.5) priors for the fixed species effects  $\beta_{[\pi]}$  and  $\beta_{[p]}$ , which are both interpretable as the logit of a proportion. We used Half-Normal(0, 1) priors for all standard deviations  $\sigma$  and a LKJCorr(2) prior for the correlation matrix  $R$ . Finally, for the negative-binomial shape parameter  $\varphi$ , we used a Half-Normal (0, 1) on its inverse ( $1/\varphi$ ), as recommended in <https://github.com/stan-dev/stan/wiki/Prior-Choice-Recommendations>.

#### *Model with lines random effects only*

The second model fitted is nearly identical to the one above, except that there is no species-level fixed effects anymore, only overall intercepts:

$$\mu_{s,l} = \beta_{0[\mu]} + \alpha_{[\mu]l},$$

$$\text{logit}(\pi_{s,l}) = \beta_{0[\pi]} + \alpha_{[\pi]l},$$

$$\log(\lambda_{s,l}) = \beta_{0[\lambda]} + \alpha_{[\lambda]l},$$

$$\text{logit}(p_{s,l}) = \beta_{0[p]} + \alpha_{[p]l}.$$

The remainder of the model, including priors is otherwise unchanged.

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## Article 2: Life-history variation shapes the speed and internal dynamics of expansion in three *Trichogramma* wasp species

Chloé Guicharnaud, Géraldine Groussier, Laurent Lamy, Théo Delauney, Théo Hedelin, Erwan Beranger, Maxime Dahirel, Elodie Vercken

### Introduction

As more and more biological invasions or species' range shifts are recorded, being able to understand the mechanisms behind population expansions becomes increasingly important. From climate change (Parmesan, 2006; Thomas, 2010; Rubenstein et al., 2023) to accidental (Montagnani et al., 2022; Müller-Schärer et al., 2023) or voluntary (Yan et al., 2001; Schwarzländer et al., 2018) anthropogenic introductions, a species colonizing a new habitat might have negative impacts on the invaded ecosystem. After the invasion of *Mnemiopsis leidyi* in the southern Caspian Sea, probably through ballast waters from commercial ships, a huge decrease in zooplankton diversity and abundance was observed (Roohi et al., 2008), resulting in a cascading effect through trophic levels (Ivanov et al., 2000). The intentional release of the harlequin lady beetle, or *Harmonia axyridis*, resulted in a significant decrease in native ladybugs by out-competing them (Roy et al., 2012). Negative community-level effects have also been observed in climate-induced range shifts (Sorte et al., 2010a). On a more anthropocentric note, both biological invasions or range shifts have well-documented or predicted socio-economic impacts (Aukema et al., 2011; Madin et al., 2012; Rockwell-Postel et al., 2020; or see the database of the InvaCost project, Diagne et al., 2020, 2021).

Prediction tools and demographic analyses are of great help when trying to understand expansions, their underlying mechanisms, or determining the impact of those invasive populations on new environments (Wadsworth et al., 2000). Depending on the invading species dynamics, the optimal response to limit spread could either be to remove populations at the edge of the expansion (Moody & Mack, 1988; Travis & Park, 2004; Govindarajulu et al., 2005), or on the contrary aim at populations further away from the front (Tobin et al., 2011), depending on what is the main source of establishing individuals.

It was by studying the population dynamics of the spongy moth *Lymantria dispar*, that the STS (Slow The Spread) program exploited the presence of a strong Allee effect, i.e. populations under a certain threshold density have a negative growth rate and cannot establish (Tobin et al., 2009; Vercken et al., 2011; Walter et al., 2020). The program is focused on reducing intermediate populations' density, low enough to pass under the critical density value, while no management efforts are necessary for low-density satellite populations as they go extinct by themselves (Liebhold & Bascompte, 2003). However, being able to correctly predict expansion dynamics is complicated as many mechanisms may affect spread behaviour.

Range expansions are places where peculiar and rapid evolution can occur and may lead to huge variations between the original core population and edges. As a population moves forward, multiple non-stochastic evolutionary processes may modify the values or spatial distribution of traits involved in the spread, be it growth or dispersal (Travis et al., 2009; Therry et al., 2015; Jan et al., 2019). Spreading populations can be subjected to spatial sorting (Cwynar & MacDonald, 1987; Phillips & Perkins, 2019), where trait variation is spatially selected from core to front, or more well-known natural selection (Holt et al., 2005). Those mechanisms may lead to an evolutionary shift towards higher dispersal abilities as we get closer to range edges (Ochocki & Miller, 2017; Weiss-Lehman et al., 2017; Fronhofer et al., 2017), and may also lead to a higher reproduction rate in front populations (Szűcs et al., 2017; Van Petegem et al., 2018). Many studies showed that trait evolution can lead to a higher-than-expected spread based on original trait values, as seen in e.g. Ochocki & Miller (2017) or Williams et al (2016). A major issue is that biological expansions are subjected to both environmental and demographic stochastic events (Lande, 1993), which can increase the variability between different expansions (Williams et al., 2019), and reduce our predictive power. However, biological invasions are generally unique and unreplicated events, and experimentally releasing non-native species in the wild to increase replication is often unethical, given the aforementioned ecological or economic. In that context, insights gained from experimental expansion replicates in controlled conditions or simulations to gain insights on mechanisms driving the spread are instrumental for understanding spread mechanisms.



Another factor playing on the difficulty to predict spread dynamics is context dependence. If we look at density-dependence, expansions have been classified into a continuum of "pushedness", going from "pulled" to "pushed" expansion types (Stokes, 1976; Bonnefon et al., 2013; Birzu et al., 2018; Gandhi et al., 2019). Pulled expansions occur when the spread is mostly the result of growth and dispersal of the low-density population at the edge of an expansion, "pulling" forward the rest. Pushed waves by contrast are characterized by a spread mostly fed by high-density populations more behind the front, "pushing" the whole population to move forward. Both positive density-dependent dispersal (Birzu et al., 2019; Zhu et al., 2023) and the presence of Allee effects (Lewis et al., 2016; Erm & Phillips, 2020) can generate pushed waves. Different expansion dynamics have been shown to occur depending on the degree of pushedness (Garnier et al., 2012), affecting both the genetic (Gandhi et al., 2019; Birzu et al., 2021) and demographic (Williams et al., 2019) aspects of an expansion, reflected by variation in evolutionary and adaptive responses, population distribution, or dispersal patterns. All those differences may need to be included when determining the best management plan. Neutral genetic diversity tends to be reduced for pulled expansions compared to pushed ones, as individuals from more diverse, high-density populations, disperse to the edge and maintain the genetic diversity at the front (Roques et al., 2012; Birzu et al., 2019; Gandhi et al., 2019). We can also expect different population distributions in space, with theoretically steeper density clines from core to front for pushed wave (Gandhi et al., 2019). Studies on how eco-evolutionary feedback may intertwine with expansions pushedness have started to emerge; Erm and Phillips (2020) demonstrated how the evolution of an Allee effect-resistant trait shifted pushed expansions into becoming more pulled, while [Appendix 1](#) showed how on top of the environmental context, varying evolutionary patterns of dispersal and its sources led either to pushed expansions becoming more pulled, or for expansions to become even more pushed (or alternatively pulled) as time pass.

However, these previous studies tend to overlook one important factor, that is trait covariation: if both population growth and dispersal traits can shape the dynamics of range expansions, what happens when they are phenotypically or genotypically linked, as is often the case (Ronce, 2012; Bonte & Doherty, 2017)? Examples of "colonizer syndrome",

where individuals with high dispersal abilities, rapid development time and high fecundity become dominant in newly populated habitats (Baker & Stebbins, 1965), have been observed in the course of natural range expansion (Saastamoinen, 2007a; b; Tabassum & Leishman, 2018; Clark et al., 2022). Other studies showed that dispersal-reproduction trade-off may limit the simultaneous increase in both high dispersal and high reproduction at range edges (Hughes et al., 2003; Gu et al., 2006; Burton et al., 2010; Kelehear & Shine, 2020; Urquhart & Williams, 2021). Those studies were mainly focused on trade-offs and other syndromes linking reproduction and dispersal (Clobert et al., 2012; Bonte & Doherty, 2017), as those two traits are the two main drivers of expansion. However, other axes of trait covariation may affect evolution during spread, such as the pace-of-life axis. The pace-of-life corresponds to one variation axis where organisms can be placed along a continuum going from "slow" to "fast" type (Stearns, 1983; Braendle et al., 2011). "Slow" types can be defined as organisms with long lifespans and development times but low reproduction, while "fast" types have shorter lifespans and development times for higher reproductions (Bielby et al., 2007; Gaillard et al., 2016). This axis, found in many studies spanning a multitude of taxonomic ranks (Williams et al., 2010; Auer et al., 2018; Healy et al., 2019), might be important to account for in expansion dynamics. One type may be more favoured than the other in the core or at the front of an expansion, led by the variation of density and level of stochasticity between the two locations. In Wright et al. (2019) the authors suggest that slow types will have a greater fitness as density increases because of higher inter-specific competition resistance, while high reproductive fast types will do better at the low-density, highly stochastic range edge. They also propose that fast types should benefit more from positive density-dependent dispersal, as to settle at those favourable low densities. As the pushedness of an expansion theoretically highly influences density patterns, a possible interaction between the pace of life and the pulled versus pushed concept need to be studied, as it can be helpful in determining what will happen in expansions.

The goal of this paper is to observe how the initial trait structure, through the position in the pace of life and its interaction with dispersal abilities, may evolve during expansion and impact the pushedness of said expansion. For this, we compare both the ecological and evolutionary dynamics of three species of *Trichogramma* wasps spreading in

replicated experimental expansions for 11 generations. The three selected species vary in their initial position on the pace-of-life axis (Guicharnaud et al., 2023); as slow types have better inter-specific competition resistance, and so a better fitness at high density than faster types, we expect that the slower a *Trichogramma* species is, more pushed will be the expansion generated, with a positive density-dependence in growth and/or dispersal. As the expansion continues and generations pass, we expect a selection of faster individuals with higher dispersal abilities within slow populations through density selection at range edges and spatial sorting. Replicated expansions will allow us to compare the repeatability of expansion spread between species. We expect to see a lower variance between replicates for slower species, as the contribution of individuals behind the front and higher, less fluctuating densities or bottlenecks at the front should lower variance-inducing mechanisms such as genetic drift (Birzu et al., 2018; Williams et al., 2019).

## Materials and methods

### *Biological material*

*Trichogramma* (Hymenoptera: Trichogrammatidae) wasps are small (adult length < 1 mm) haplodiploid egg parasitoids. As some of their hosts are pest species, *Trichogramma* is frequently used in biological control against Lepidoptera pests (Smith, 1996; Consoli et al., 2010; Sigsgaard et al., 2017). Many characteristics make them a good choice for microcosm experiments: their small size, their short generation time (around 15 days at 22 °C), their ease of rearing and maintenance under standard lab conditions, and the ready availability of many lines per species (Marchand et al., 2017). When reared on *Ephestia kuehniella* moth eggs, only one viable descendent generally emerges at the end of development (Corrigan et al., 1995), and parasitized eggs are easily identifiable by the chorion turning black around 5 days after parasitism, a direct result of released melanin from the developing larvae (Pintureau & Petinon, 1999). Population sizes can therefore be reliably assessed while wasps are still within their hosts, by counting dark host eggs.

We selected three of the five *Trichogramma* species tested for their pace-of-life in Guicharnaud et al (2023): *T. brassicae* Bezdenko, 1968 a "fast" species with fast

development and high fecundity, *T. bourarachae* Pintureau & Babault, 1988 a "slow" species with slower development and lower fecundity, and *T. semblidis* (Aurivillius 1898), as an intermediate species that tends towards the fast end of the gradient. We initially considered an additional fourth species, *T. evanescens*, which was in Guicharnaud et al. (2023) a "slower intermediate" species; however, crossings (see below) were unsuccessful and the species was therefore discarded.

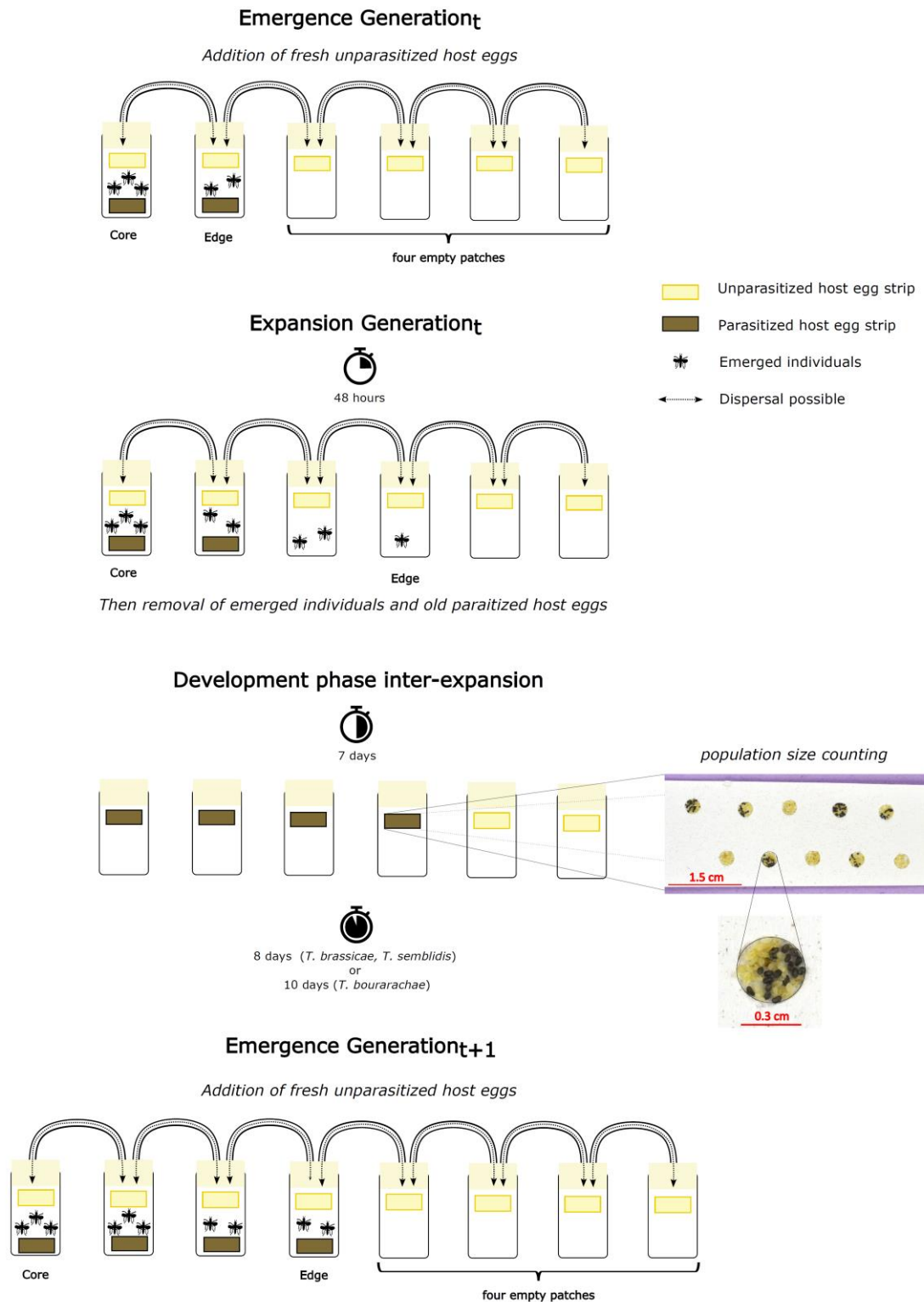
For each species, we randomly selected three sexual lines among the lines available in the Biological Resource Center (Marchand et al., 2017) and previously studied in Guicharnaud et al. (2023) (see [Supplementary Table II-2](#) for more information). We then applied the crossing protocol presented by Fellous et al. (2014) to obtain one genetic mix per species where the three source lines are expected to be equally represented genetically. This was done to ensure the presence of some standing genetic variation for evolution to occur. Throughout this initial procedure, and afterwards during the expansion experiment (see below), we used irradiated eggs of the Mediterranean flour moth *Ephestia kuehniella* (Lepidoptera: Pyralidae) as hosts (St-Onge et al., 2014) and kept the populations under standard conditions (22 °C, 70 %  $\pm$  10 % relative humidity, L:D 16:8). Individuals were additionally fed honey, presented in lines small enough to prevent drowning.

#### *Experimental range expansions*

We constructed one-dimensional stepping-stone landscapes by connecting plastic vials (10 cm height, 5 cm diameter) to one (first and last vial) or two neighbours with flexible plastic pipes (40 cm length, 5 mm of effective diameter), with an initial landscape length of 5 vials. We introduced an initial population of around 300 (ranging from 292 to 316) host eggs parasitized by *Trichogramma* at one end of the landscape, and let them expand for 11 non-overlapping generations after emerging, inclusive of the initial population (which was counted as generation 1, so generations 1 to 11). The experiment was replicated 8 times per species under standard conditions. For each generation, we proceeded as follows ([Figure II.8](#)):

- As the new generation begins to emerge, the vials are reconnected to reform the same experimental landscape, with the same order of vials. During this step, we expand the landscape if necessary to have at least four empty vials ahead of the front, leaving room for expansion. In each vial, we introduce a new paper strip with around 450 host eggs alongside a non-limiting amount of honey.
- Each generation is allowed to mate and disperse undisturbed for 48h in the landscape after connecting the vials. At the end of the allotted time, the old paper strips from which the current generation emerged are removed, all individuals are collected for future phenotyping and genotyping studies (beyond the scope of this study), and the most recent paper strips are put into new clean plastic vials, which are left unconnected for the duration of the development time. This development time was fixed at 17 days for *T. bourarachae* and 15 days for *T. brassicae* and *T. semblidis*, as to begin the next generation when each species start emerging and having a flexible time for every generation was not doable for time and organisational reasons.

A week after isolating paper strips for the development phase, host eggs that were parasitized have turned black. It allowed us to visually identify successfully parasitized eggs. For this, each egg strip was photographed (resolution: 210 6016 × 4016 pixels, for a real field of view size of around 12 × 8 cm) using a Nikon D750 211 camera (lens: AF-S Micro NIKKOR 60 mm f/2.8 G ED) fixed 37 cm above it. All parasitized eggs from every strip were manually counted using ImageJ (Schneider et al., 2012).



**Figure II.8: Summary of the different steps used for experimental expansions, to complete a generation cycle.**

Insert (right): Picture of paper strip present in vials, with parasitized (blacken) and unparasitized host eggs, one week after the end of the expansion phase.

### Demographic pushedness indicators

We generated and analysed several metrics that we expected to be associated with or influenced by the pushedness of an expansion, based on previous studies.

#### Front position and expansion velocity

The front position for generation  $t$  corresponds to the position of the furthest vial in which parasitized host eggs were observed in pictures (with the vial at one end of the landscape in which the initial population was released corresponding to position zero). Expansion velocity represents the mean number of patches colonized per generation and is estimated from statistical analyses of front position through time. As we know that density-dependent dispersal at low density is constant for all three species (Guicharnaud et al., 2023), and assuming that all species are initially pulled, expectations should be that the one species with higher population growth at low density is the fastest. Any deviation from that null expectation may signal either an unknown effect of evolution or that at least one species is pushed.

#### Median population ratio

For each generation, we defined the median population ratio of an expansion as the location of the median individual, relative to the position of the front. In theory, the succession of low-density founding events at the front present in pulled expansions should shift the position of the median individual toward the range core (ratio  $< 0.5$ ), while the more constant density pattern in pushed waves should lead to a median position closer to the centre of the landscape (ratio  $\approx 0.5$ ) (Williams et al., 2019).

#### Edge density ratio

This metric compares the population density of the front at generation  $t$  to the density (still at time  $t$ ) of the patch that was at the front during the previous generation  $t-1$  such as density ratio  $= \frac{Nt_{front\ t}}{Nt_{front\ t-1}}$ . This ratio is based on the expectation that new populations in pushed expansions are typically founded by larger numbers of individuals than in pulled expansions (Williams & Levine, 2018); hence, population size differences

between current and previous fronts should be less marked in pushed than pulled contexts.

### *Phenotypic measurements*

To understand how phenotypic traits and their density-dependence varied (or not) between species and due to the expansion process, we measured phenotypic traits at the start and the end of the experiment under two different densities. For each replicate, at the end of the 48 hours allotted for the expansion phase, we isolated wasps into new vials and offered them a fresh egg strip to parasitize in a common garden. We used this procedure for wasps from the initial released population (generation 1), and from wasps in the core patch and the frontmost patch at the end of the experimental expansion (generation 11). These wasps were kept in isolated vials and standard conditions for two generations to amplify the number of individuals before the beginning of the phenotypic experiment.

For each population sampled (the initial population and core/front of the last generation), the phenotypic experiments happened as follows ([Figure II.9](#)):

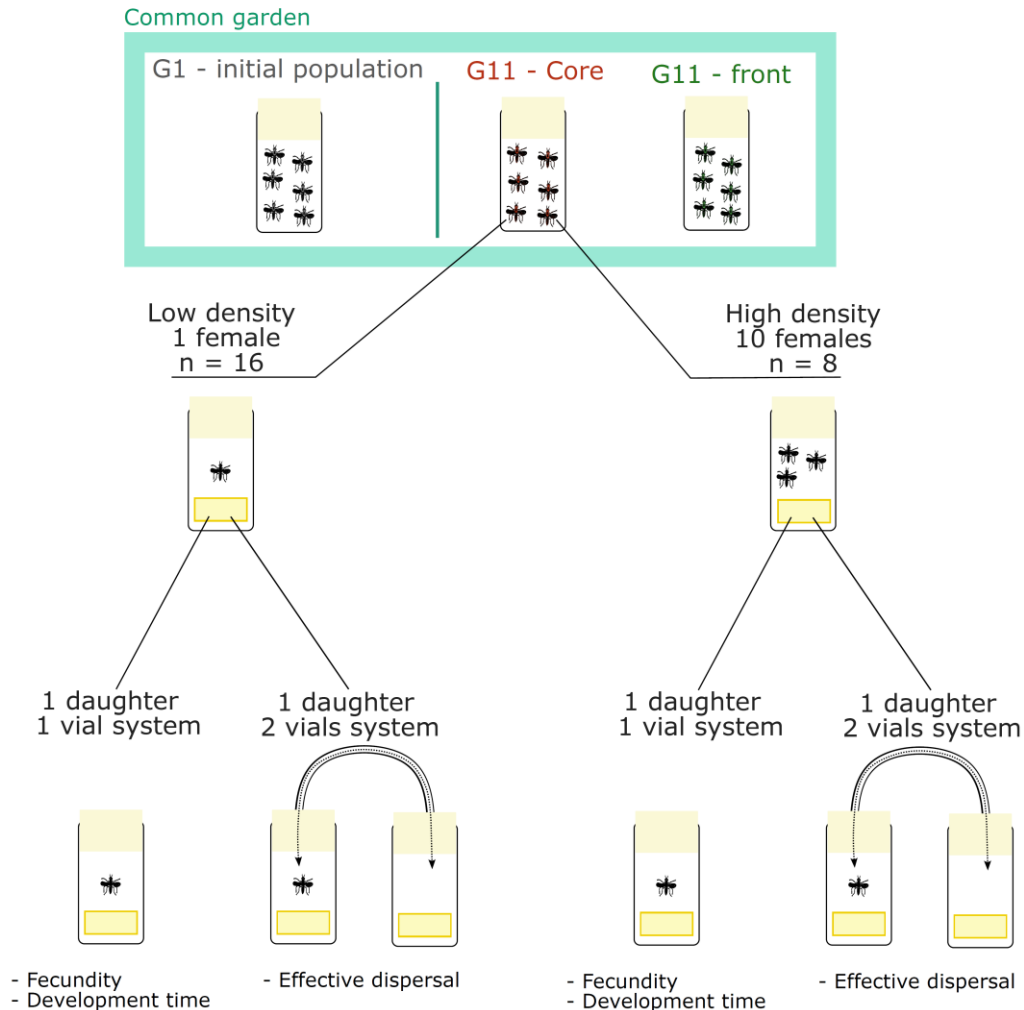
Either one or ten mated females were randomly selected among the individuals from the common garden and placed in a plastic vial (10 cm height, 5 cm diameter) alongside honey and around 90 host eggs in a paper strip. As the maximum mean fecundity for one female is rarely above 70 and at best around a hundred on *E. kuehniella* (Özder & Kara, 2010; Guicharnaud et al., 2023), the 1 versus 10 females correspond to two different mother densities, therefore a variation in larval competition (more than one egg per host, or superparasitism); Even though only one viable descendent emerges at the end most of the time, superparasitism does happen (Corrigan et al., 1995) at high densities, while it tends to be avoided for single females when the number of host eggs allows it (Wang et al., 2016). The single mother modality was replicated up to 16 times per landscape × location (start, core, front) combination (range: 1 to 14, mean: 7.2) and multiple mothers up to 8 times (range: 1 to 8, mean: 6.7), with variation due to lack of available females in some conditions (see [Supplementary Table II-3](#) for more details on replicates distribution).



For fecundity measurements, one offspring female is randomly selected for each modality and left in a plastic vial for 48 hours with around 90 host eggs on a strip and a non-limiting amount of honey. At the end, the egg strip is collected and isolated. After one week, those strips are photographed and parasitized host eggs are counted. During the 48 h, there is the possibility to observe egg retention, where females do not oviposit even when all favourable conditions to do so are met. This behaviour was already observed for *Trichogramma* species studied here (Fleury & Boulétreau, 1993; Reznik et al., 1998, 2001; Guicharnaud et al., 2023) and therefore taken into account during data analyses (see below).

Our development time measurements correspond to the mean number of days between the beginning of the 48 hours during which the female can lay eggs and the moment offsprings emerge. For that, we checked all isolated egg strips every day after taking the pictures to measure fecundity. We counted the number of descendants that emerged per day per female, before reisolating the egg strip now free of newly emerged offspring to be checked again the next day, and so until 3 successive days without emerging individuals passed. The uncertainty on when during the first two days eggs were actually laid was accounted for during our analyses of the mean number of days per female (see Data analyses).

Finally, we observed effective dispersal by isolating another female offspring from each modality in a two-vial system: the female is put into a landscape similar to the one used during expansion, but composed of only two connected vials, each containing around 90 host eggs on a paper strip and an unlimited amount of honey. The female was left in this system for 48 hours, and we considered that the female have effectively dispersed if at least one parasitized host egg was found in the second vial.



**Figure II.9: Summary of the experimental design used to measure phenotypic traits.**

The same protocol was followed for each location sampled (i.e. initial population, core and front populations at the last generation), except for core and front locations of *T. brassicae*, where there were not enough females for doing any high densities measures.

### Statistical analyses

To understand how phenotypic traits evolved, our demographic metrics values, the possible correlation between all our metrics and the repeatability of expansions, we used Bayesian multilevel/mixed models, through the *brms* R package version 2.19.0 (Bürkner, 2017a), a front-end for the Stan language (Stan Development Team, 2022), using R version 4.3.0 (R Core Team, 2023). For each model we ran, we used four chains running for 4500 iterations with a warmup of 2000 iterations. Good convergence and effective sample size were checked using the  $\hat{R}$  and bulk effective sample size proposed by Vehtari et al. (2021). Priors mostly followed McElreath (2020) with a few exceptions based on previous similar experiments on the same biological models (Dahirel, Bertin, Haond, et al., 2021;

Guicharnaud et al., 2023). See the "Data and code availability" section for links to an archived version of the annotated model code.

Phenotypic traits (effective dispersal, development time and fecundity) were each analysed using Generalized Linear Mixed Models (GLMMs) with three-way interactions between species (3 levels), position (3 levels) and maternal density (2 levels) as fixed effects, and landscape-level random effects of position and density (with no interactions). Effective dispersal used a Bernoulli model with a logit link, and development time, as a time-to-event measure, used a Log-Normal model, with an added 48 h wide interval censored to account for the uncertainty about when host eggs were actually parasitized during the 48 h experiment. As in Guicharnaud et al. (2023), a Zero-inflated Negative binomial distribution was used to account for overdispersal and an excess of zero observed in fecundity data. This excess of zeroes was modelled using a Bernoulli distribution and is biologically explained to be a consequence of egg retention during the experiment, already observed in *Trichogramma* to last over two days (Reznik et al., 2001). The second component of this sub-model used a Negative binomial distribution and represents female fecundity in the absence of retention, often abridged to "fecundity" in this paper, while the fecundity accounting for egg retention will always be referred to as "overall fecundity". Note that for effective dispersal, only random landscape-level intercepts were included as random effects, due to the limited number of dispersal events to analyse.

Demographic metrics (front density ratio and median ratio) were similarly analysed using GLMMs with the species as a fixed effect (3 levels), and a landscape-level random intercept. A beta-binomial model with a logit link was used for front density ratio analyses, with data limited to generations where expansion occurred, using the combined density of the front and the previous front position as the number of trials. A binomial model with a logit link was fitted on the median ratio. Front location at time  $t$  was analysed using a linear mixed model with fixed and random intercepts fixed to 0 (as only the starting patch with  $x=0$  is populated upon release), with species-specific slopes of time as fixed effects, and landscape-specific slopes of time as random effects. For the model analysing front location only, landscape-level random effect variances and residual variance were allowed to vary between species. This allowed us to estimate variance partitioning metrics such as

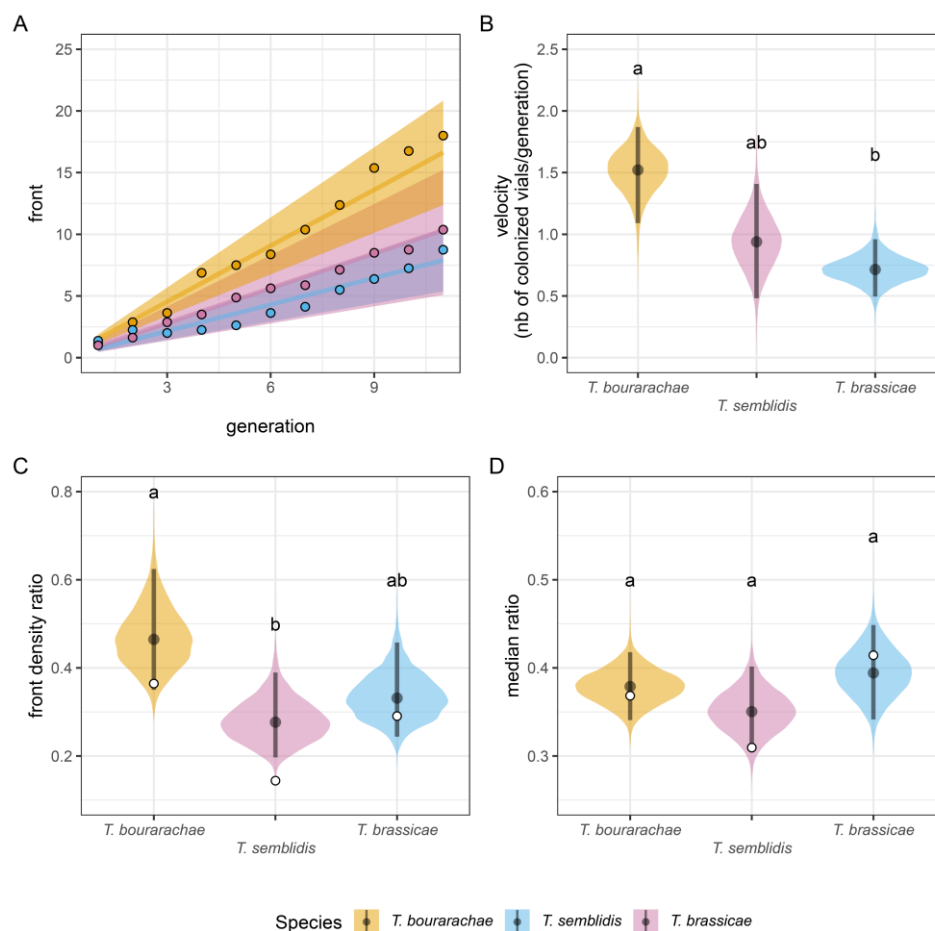
conditional and marginal  $R^2$  for each species separately and compare them. Conditional  $R^2$  correspond to the proportion of model variance explained by predicted random and fixed effects, while marginal  $R^2$  looks at the proportion of variance explained by fixed effects only (Gelman et al., 2019). We did not estimate conditional and marginal  $R^2$  for the density ratio due to the absence of guidelines in the reference literature (Nakagawa & Schielzeth, 2013; Johnson, 2014; Nakagawa et al., 2017) for beta-binomial models. Finally, we used a Binomial generalized linear model to determine whether species differed in the proportion of all parasitized eggs that were found outside the initial patch at the end of the first generation, which can be seen as a measure of effective dispersal at high current density (as opposed to effective dispersal at high maternal/larval density obtained from the experiments described in "Phenotypic traits measurement").

To understand how these trait and demographic metrics were correlated, we initially included all metrics that were measured repeatedly at the replicate landscape level (i.e. all except the last one), into one multivariate model to observe landscape-level correlations between all response variables once species identity and other fixed effects are accounted for. For the most part, we found no evidence for landscape-level correlations between traits and/or demographic parameters (see Supplemental Material 5 for more information), we present here the results from the separate univariate models only.

## Results

### *Faster expansion, higher gene flow and a tendency for less stochasticity in *T. bourarachae**

On average, *Trichogramma bourarachae* expanded its range faster than *T. brassicae*, with *T. semblidis* as an intermediate species (Figure II.10 A, B). *T. bourarachae* showed a higher front density ratio than *T. semblidis*, but no species differences were found for the median ratio (Figure II.10 C, D). Moreover, *T. bourarachae* presented the highest effective dispersal rate at high current densities of the three species with half of the parasitized eggs after the first generation found outside of the initial vial (Figure II.11).



**Figure II.10: Posterior values as a function of the *Trichogramma* species**

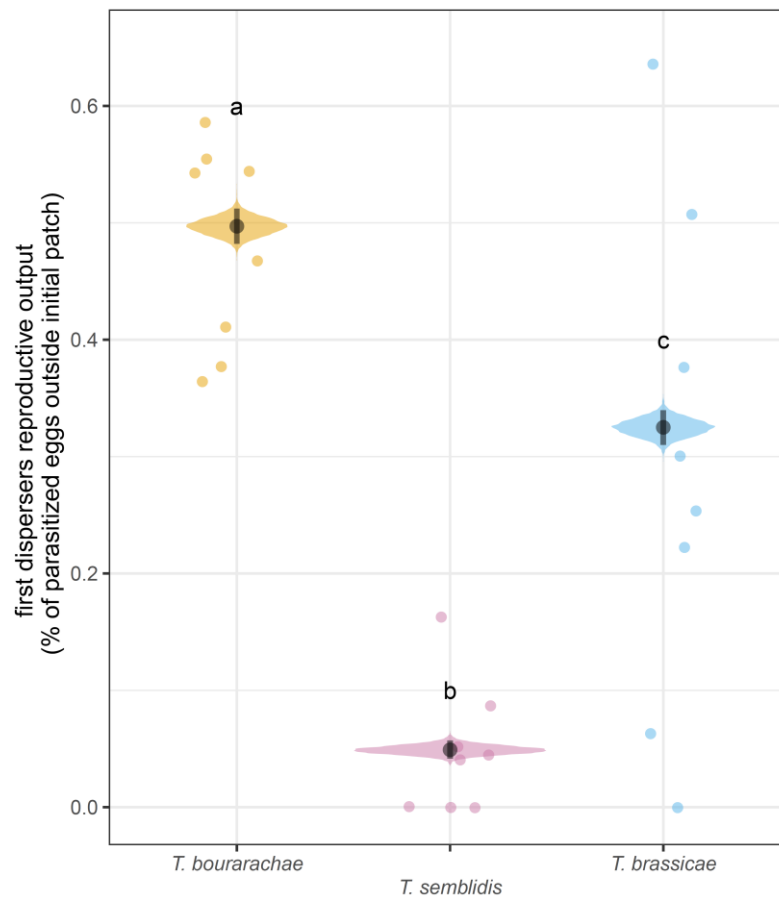
Representing A) the front position at every generation, B) the velocity of expansions, C) the ratio between the actual front population and the density in the position of the previous front, and D) the ratio between the median population position and the front. The 95 % highest density interval and the posterior mean per species are represented by black bars and dots, while the white dots represent observed mean values for illustrative purposes. As the velocity is a slope parameter extracted from the front position sub-model, no observed values were deemed necessary. For a given trait, two species with no index letters in common are considered to have "significant" pairwise comparison differences based on whether or not the 95 % highest density intervals on linear predictors included zero.

The model for the front location was able to explain a large part of the total variance (a proportion over 0.87 based on conditional  $R^2$ ), but partitioned differently within species (**Table II-4**); *T. bourarachae* tends to be the least stochastic overall with an inter-landscape variance proportion of 0.35 ( $R^2c - R^2m$ ) and 0.06 for intra-landscape ( $1 - R^2c$ ), compared to *T. semblidis* (inter-landscape variation= 0.66; intra-landscape= 0.07) and *T. brassicae* (inter-landscape variation= 0.40; intra-landscape= 0.14).

**Table II-4: Marginal and conditional R<sup>2</sup> values of the front position response per species.**

Those values were calculated on a univariate model with the same model formula as in the front sub-model presented in Material and Method. Values in brackets represent the 95 % highest density intervals.

Species	Conditional R <sup>2</sup>	Marginal R <sup>2</sup>
<i>T. bourarachae</i>	0.94 [0.91; 0.97]	0.59 [0.29; 0.82]
<i>T. brassiaca</i>	0.87 [0.79; 0.95]	0.47 [0.22; 0.69]
<i>T. semblidis</i>	0.93 [0.88; 0.98]	0.27 [0.06; 0.50]



**Figure II.11: Posterior values of the proportion of parasitized eggs present outside of the initial vial over the total number of parasitized eggs at the end of the first generation.**

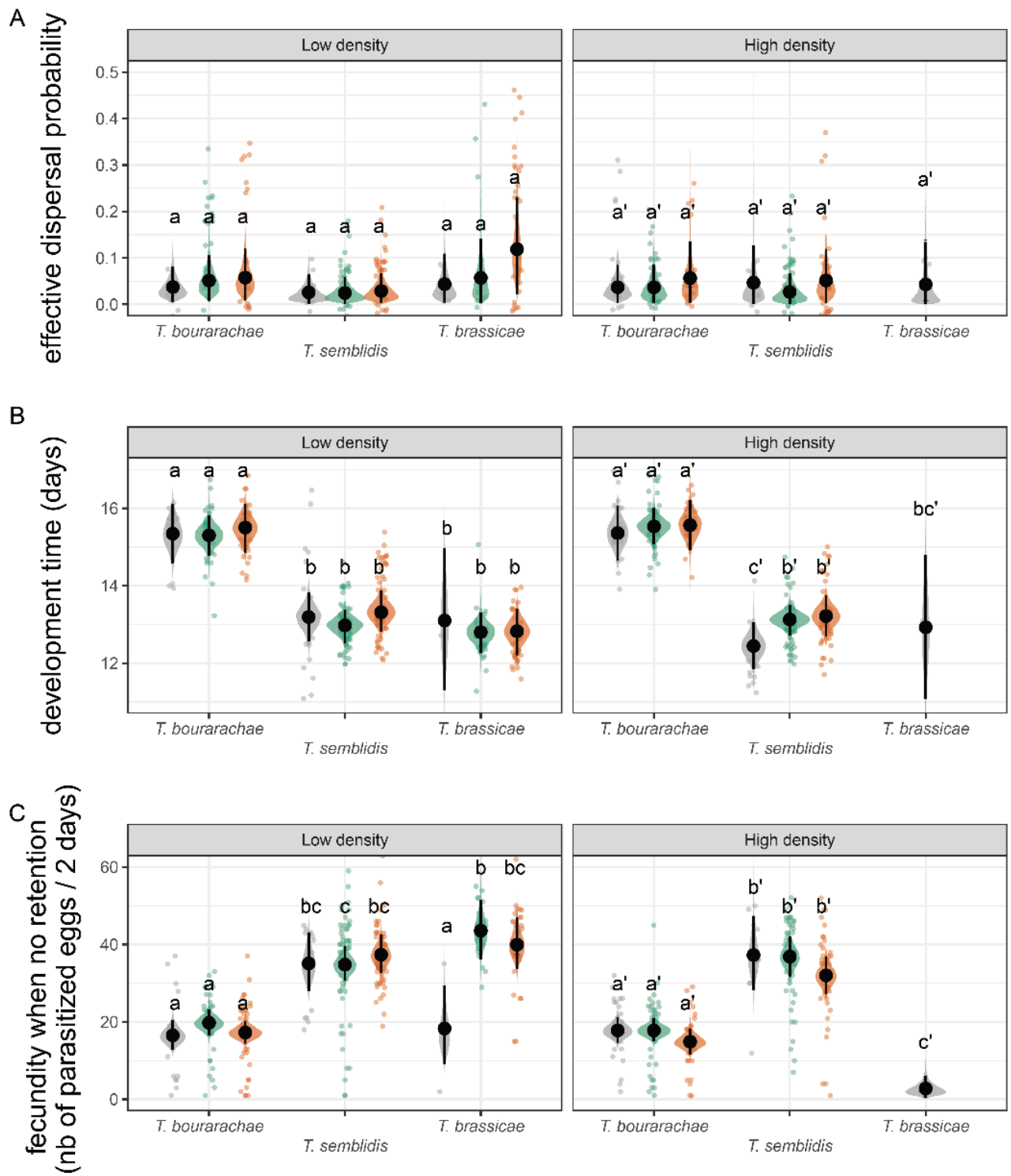
The 95 % highest density interval and the posterior mean per species are represented by black bars and dots, while the white dots represent observed mean values for illustrative purposes. For a given trait, two species with no index letters in common are considered to have "significant" pairwise comparison differences based on whether or not 95 % highest density intervals on linear predictors included zero.

*Low variation in time on phenotypic trait values*

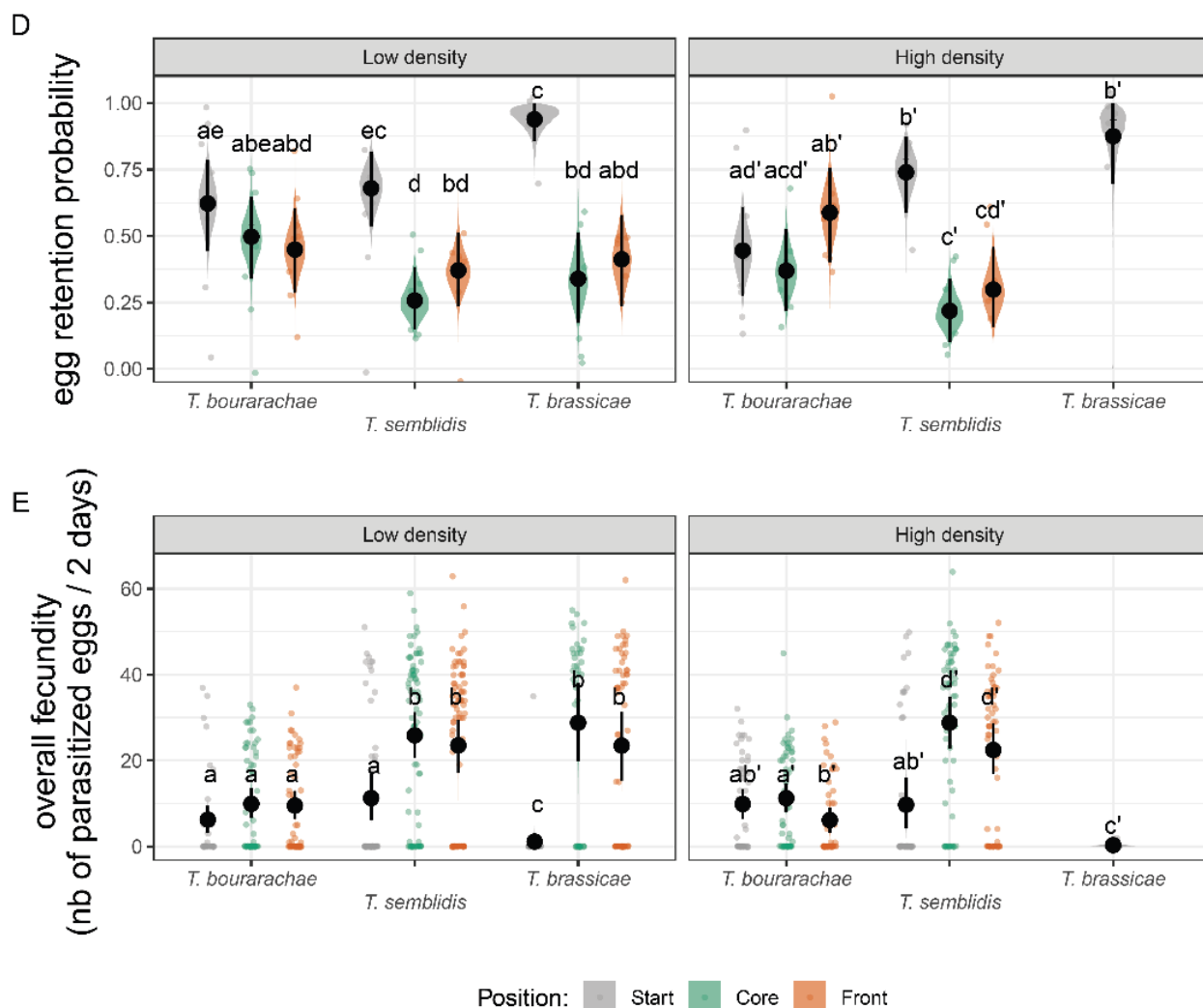
*T. bourarachae* has significantly higher development times at both densities (**Figure II.12 B**), for lower fecundity values overall (both fecundity and overall fecundity; **Figure II.12 C, E**). *T. brassicae* initial populations presented extreme reproduction trait values with low fecundity (near zero at high densities) and high retention times (**Figure II.12 C, D, E**). When comparing initial to Core/Front populations, all species tended to evolve lower egg retention probability for higher overall fecundity (**Figure II.12 D, E**). No differences were found in effective dispersal traits (**Figure II.12 A**).

*Density-dependence on phenotypic traits*

In starting populations, development time was faster at high maternal densities compared to single mothers in *T. semblidis* (**Figure II.13 B**), and fecundity was lower for *T. bourarachae* (while overall fecundity is not different than zero, it also tends to be lower; **Figure II.13 C, E**). In *T. bourarachae*, density-dependence in overall fecundity differed between initial and front populations, from slightly positive in the former to slightly negative in the latter (**Figure II.13 E**). However, neither was clearly different from zero. For *T. bourarachae*, we found that density-dependence in egg retention probability varied between the front (slightly positive) and the two other populations (slightly negative). We found no evidence for other differences in density dependence across traits, populations, and species (**Figure II.13**).



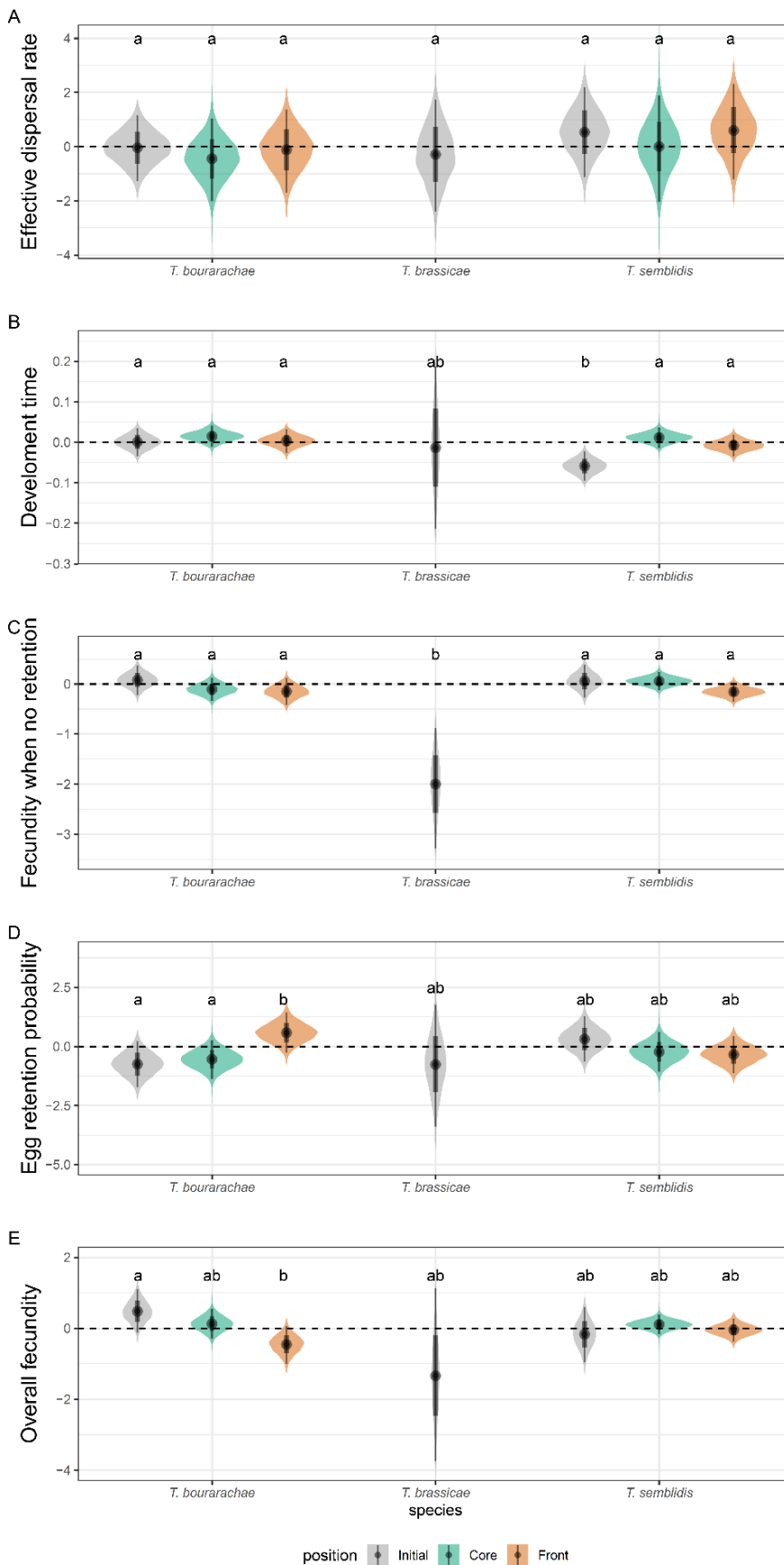




**Figure II.12: Posterior values of phenotypic traits as a function of the species, position and mothers' density.**

Each sub-plot corresponds to one trait: A) The effective dispersal rates in 48 h, B) the mean development time of all offspring in days, C) the number of eggs parasitized by one female in two days, D) the probability of egg retention during the experiment and E) overall fecundity value, when both fecundity and retention time are accounted for. The 95 % highest density interval and the posterior mean per modality combination are represented by black bars and dots, while the white dots represent observed mean values for illustrative purposes. For a given trait, among one density setting, two combinations with no index letters in common are considered to have "significant" pairwise comparison differences on linear predictors based on whether or not 95 % highest density intervals included zero.

Density effect on:



**Figure II.13: Pairwise comparison values on high versus low densities per species/position combination for the different measured traits**

A) The effective dispersal rates in 48 h, B) the mean development time of all offspring in days, C) the number of eggs parasitized by one female in two days and D) the probability of egg retention during the experiment and E) the overall fecundity in two days. The absolute comparison was done on traits linear posteriors. Values in brackets represent the 95 % mean quantile interval. The horizontal line represents zero differences between high-low densities. If under zero, trait values are lower at high mother densities than at low mother densities.

## Discussion

### *A partial correlation between pushedness and slowness*

*T. bourarachae*, the slowest on the pace-of-life axis, as confirmed by long development time and low fecundity observed in **Figure II.12** B, C, presented the highest values of front density ratio (**Figure II.10** C) and initial population reproductive output outside of the first vial (**Figure II.11**), a tendency for less among and within landscapes stochasticity in the front position (**Table II-4**), and positive density dependence on overall fecundity in initial populations (**Figure II.13** E). Those partial results agree with our hypothesis that slower species in the pace of life should lead to more pushed expansions. The higher edge density ratios (**Figure II.10** C) can be a result of a lower growth at low density for slow species, a result of a trade-off for better intraspecific competition resistance (Wright et al., 2019). In the front, at low density, slow species should therefore present a lower-density contrast between the old front after one generation and the actual front.

The lower inter- and intra-landscape variance on the front position (and so expansion velocity) in the expected more pushed *T. bourarachae* showed similar results to the front wandering in pulled versus pushed expansions in Birzu et al. (2018). This pushed expansion behaviour can be linked to slower species and higher population stability presented in Wright et al. (2019). As a population expand, fewer events of either extinction or long-distance establishment can occur if the overall meta-population is stable and not prone to high-density fluctuations in time and space, as it is the case in fast species.

As presented in the introduction, pushed expansions are generated by positive density-dependence on fecundity (presence of an Allee effect) or dispersal. We can observe in **Figure II.13** E that the initial population of *T. bourarachae* tend toward a positive density dependence in overall fecundity, while *T. brassicae* populations tend toward a negative density dependence. It fits the expectations of Wright et al. (2019) when presenting the lower Malthusian fitness of slow species at low density, but with a higher fitness at high density compared to faster species. If we look at the effect of density in core versus front populations in the same figure, we can observe in *T. bourarachae* a shift from more

positive to more negative density-dependence while the effect on core populations does not vary (consistent with observation also on *Trichogramma* in Dahirel, Bertin, Calcagno, et al., 2021). This result confirms the observations on simulated populations in Erm & Phillips (2020) of the evolution of an Allee effect-resistant trait in edge individuals. This evolution transformed initially pushed expansions into pulled expansions and can be one factor explaining why our expansion metrics lack power and the slight acceleration of the front position during the last generations in *T. bourarachae* (Figure II.10 A). This shift correlates with the expectation of finding faster individuals at the front (Fronhofer et al., 2017; Van Petegem et al., 2018).

#### *Density-dependence dispersal can alter expectations*

One demographic metric in opposition to expectations based on phenotypic traits values only was the position of the front, or spread velocity (Figure II.10 A, B): *T. bourarachae* presented the fastest advancing front of the three species studied, while our expectation based on its pace-of-life position suggested a slower spread, as it presents the lowest reproductive output at low densities (Figure II.12 C, E). The reason behind the higher velocity in *T. bourarache* could be the presence of positive density dependence in dispersal. If we look at our experiment on effective dispersal between different mother densities, we observe an absence of mother density-related effects (Figure II.12 A). However, an indirect comparison between the effective dispersal probability of one female alone (corresponding to phenotypic measure experiments) and the effective dispersal of the initial population of 300 individuals during the expansion phase (the only generation where we know the original position of every individual) presented signs of positive density-dependent dispersal for *T. bourarachae* (Figure II.11). The correlation between positive density-dependent dispersal and faster spread is consistent with Zhu et al. (2023) results, where spread rates increased with density-dependent dispersal, for any fixed values of density-dependent fecundity.

Our results also demonstrate that estimating expansion velocity based only on mean trait values without accounting for all density-dependent mechanisms is not reliable. It showed how while positive density-dependence in growth or dispersal could both be the source of a pushed behaviour (Birzu et al., 2019), we need to further develop our knowledge on

how each mechanism can interact and change expectations depending on their contribution to spread. Also, as high-density dynamics behind the edge influence the expansion through this positive density dependence (Bonnenfon et al., 2014; Gandhi et al., 2019), this paper supports the importance of keeping the whole expansion profile when studying pushed dynamics, as stable core populations way behind the expansion edge might still heavily participate in the spread.

#### *Low variation in time on phenotypic trait values*

The evolution of development time was largely constrained by the experimental protocol that enforced a fixed number of days between two consecutive generations and then allowed only a window of 48 hours to emerge, mate and disperse. For *T. semblidis*, a significantly higher development time at the start of the experiment was observed for low mother densities, but no longer present at the end of the experiment (Figure II.13 B). While the absence of density-dependence and higher development times at the last generation for high mother densities (Figure II.12 B) is probably the result of the experimental design, the fact that this initial density-dependence is observed in only one species is interesting. As in *Trichogramma*, males tend to emerge earlier (Consoli et al., 2010), further studies on the effect of density on sex ratio could shed some light on whether or not the differences come from sex ratio or another factor.

This restriction on development time can also explain how the high variability in development times for *T. brassicae* single mother decreases to end with more values around 13 days, possibly to have already emerged when the experiment begins on the 14th day of development. Fecundity also showed rather small variations (Figure II.12 C), except for *T. brassicae*, but as only a few individuals were able to be measured for initial populations, it is hard to determine the validity of this precise measure (see replicates distribution Supplementary Table II-3). Fecundity could stay fixed due to a strong genetic correlation with development time, leading to the protocol indirectly constraining its evolution through fixed development. It seems that overall fecundity was allowed more freedom through an evolution of egg retention probability (Figure II.12 D, E), demonstrating that the correlation is not global but specific to one fecundity component,

and playing on others can be a way to bypass strong trade-offs (Holzman et al., 2011; Garland et al., 2022).

This experiment demonstrates how we need to be cautious when fixing a precise development time, which is often the case in experimental evolution/ expansions with discrete generations (Wagner et al., 2017; Weiss-Lehman et al., 2017; Szűcs et al., 2017; Haond et al., 2021), as it can strongly limit other traits evolution. The use of simulated expansion is a widely used possibility to solve the issue of such limitations of laboratory experiments and can open the way to more precise expectations on how the pace of life and pushed/pulled expansions interact. For this, this simulated population could present density dependence on both growth and/or dispersal, trait correlations, evolution, and stochasticity. This last perspective is a demonstration of how much experiments and simulations rely on each other to counterbalance their weaknesses and help construct more precise theories.

## Article 2: Supplementary Materials

### Supplementary Material 1 - Creation of species mixes

*Trichogramma* lines used to create all mixes were selected at random from a pool of lines studied in Guicharnaud et al. (2023). We selected three lines from *T. bourarachae* ( $N_{lines} = 4$ ) and *T. brassicae* ( $N_{lines} = 9$ ), being the two most contrasted species in the pace-of-life axis, and *T. semblidis* ( $N_{lines} = 5$ ) as an intermediate. Only three species on the five studied were used for feasibility reasons. Those parental lines come from different sampling efforts, but were all collected between 2013 and 2016, and reared under the same standard conditions (18°C, 70% ± 10% relative humidity, L:D 16:8).

#### Supplementary Table II-2: Table of the 9 lines used to create the three species mixes.

The table contains lines names, along with the year of collection and GPS coordinates of the original clutch reared to create lines. All *T. brassicae* lines were shared by the biocontrol firm BioLine as part of a collaborative project (<https://www.colbics.eu/Main-Results/Intraspecific-diversity-in-Trichogramma-brassicae>), and their geographic origin is kept confidential, while every other lines came from France.

Species	Lines	Capture year	lon	lat
<i>T. bourarachae</i>	ISA11969	2016	6.90	43.82
<i>T. bourarachae</i>	ISA5544	2015	7.12	43.65
<i>T. bourarachae</i>	ISA6646	2015	6.90	43.82
<i>T. brassicae</i>	F5-8	2013	-	-
<i>T. brassicae</i>	F6-4	2013	-	-
<i>T. brassicae</i>	I6-5	2013	-	-
<i>T. semblidis</i>	PR007	2015	5.43	43.59
<i>T. semblidis</i>	FPV034_A	2015	4.88	45.95
<i>T. semblidis</i>	BL110	2016	0.89	45.2

## Supplementary Material 2 - Replicate distribution

**Supplementary Table II-3: mean number of replicates per species and treatments**

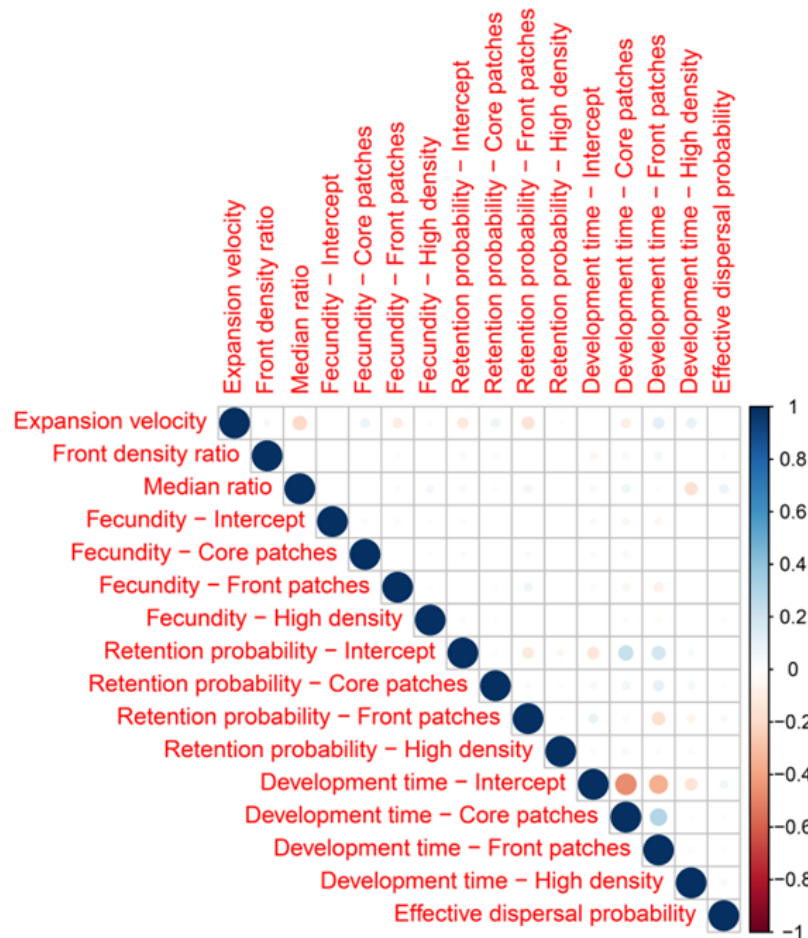
With standard deviation and range. The maximum number of replicates for single mother density is 16, and 8 for multiple mothers.

Species	Position	Mother density	Experiment	replicate nb. (mean $\pm$ SD)	range
<i>T. bourarachae</i>	Initial	Single	Dispersal	4.1 $\pm$ 1.8	2-7
<i>T. bourarachae</i>	Initial	Single	Fecundity	4.3 $\pm$ 2	2-8
<i>T. bourarachae</i>	Initial	Multiple	Dispersal	5.8 $\pm$ 0.9	5-7
<i>T. bourarachae</i>	Initial	Multiple	Fecundity	5.6 $\pm$ 0.7	5-7
<i>T. bourarachae</i>	Core	Single	Dispersal	7.0 $\pm$ 2.9	1-11
<i>T. bourarachae</i>	Core	Single	Fecundity	7.5 $\pm$ 3.3	1-12
<i>T. bourarachae</i>	Core	Multiple	Dispersal	7.4 $\pm$ 0.7	6-8
<i>T. bourarachae</i>	Core	Multiple	Fecundity	7.4 $\pm$ 1.1	5-8
<i>T. bourarachae</i>	Front	Single	Dispersal	7.3 $\pm$ 2.4	3-11
<i>T. bourarachae</i>	Front	Single	Fecundity	7.5 $\pm$ 1.9	5-10
<i>T. bourarachae</i>	Front	Multiple	Dispersal	6.0 $\pm$ 2.4	1-8
<i>T. bourarachae</i>	Front	Multiple	Fecundity	6.5 $\pm$ 2.3	1-8
<i>T. brassicae</i>	Initial	Single	Dispersal	4.0 $\pm$ 2.0	1-7
<i>T. brassicae</i>	Initial	Single	Fecundity	4.0 $\pm$ 1.7	1-6
<i>T. brassicae</i>	Initial	Multiple	Dispersal	3.1 $\pm$ 1.9	1-6
<i>T. brassicae</i>	Initial	Multiple	Fecundity	3.5 $\pm$ 1.9	1-6
<i>T. brassicae</i>	Core	Single	Dispersal	7.4 $\pm$ 1.9	5-10
<i>T. brassicae</i>	Core	Single	Fecundity	6.8 $\pm$ 3.2	1-10
<i>T. brassicae</i>	Core	Multiple	Dispersal	0.0 $\pm$ 0.0	0-0
<i>T. brassicae</i>	Core	Multiple	Fecundity	0.0 $\pm$ 0.0	0-0
<i>T. brassicae</i>	Front	Single	Dispersal	9.8 $\pm$ 2.9	5-13
<i>T. brassicae</i>	Front	Single	Fecundity	9.7 $\pm$ 2.7	5-12
<i>T. brassicae</i>	Front	Multiple	Dispersal	0.0 $\pm$ 0.0	0-0



Species	Position	Mother density	Experiment	replicate nb. (mean $\pm$ SD)	range
<i>T. brassicae</i>	Front	Multiple	Fecundity	0.0 $\pm$ 0.0	0-0
<i>T. semblidis</i>	Initial	Single	Dispersal	6.4 $\pm$ 2.5	2-8
<i>T. semblidis</i>	Initial	Single	Fecundity	6.4 $\pm$ 2.5	2-8
<i>T. semblidis</i>	Initial	Multiple	Dispersal	7.5 $\pm$ 0.5	7-8
<i>T. semblidis</i>	Initial	Multiple	Fecundity	7.7 $\pm$ 0.5	7-8
<i>T. semblidis</i>	Core	Single	Dispersal	9.1 $\pm$ 1.9	6-11
<i>T. semblidis</i>	Core	Single	Fecundity	9.3 $\pm$ 2.1	6-12
<i>T. semblidis</i>	Core	Multiple	Dispersal	7.8 $\pm$ 0.7	6-8
<i>T. semblidis</i>	Core	Multiple	Fecundity	7.8 $\pm$ 0.7	6-8
<i>T. semblidis</i>	Front	Single	Dispersal	10.2 $\pm$ 2.2	6-14
<i>T. semblidis</i>	Front	Single	Fecundity	10.5 $\pm$ 2.4	6-14
<i>T. semblidis</i>	Front	Multiple	Dispersal	7.6 $\pm$ 0.7	6-8
<i>T. semblidis</i>	Front	Multiple	Fecundity	7.6 $\pm$ 0.7	6-8

## Supplementary Material 3 - Correlations between traits

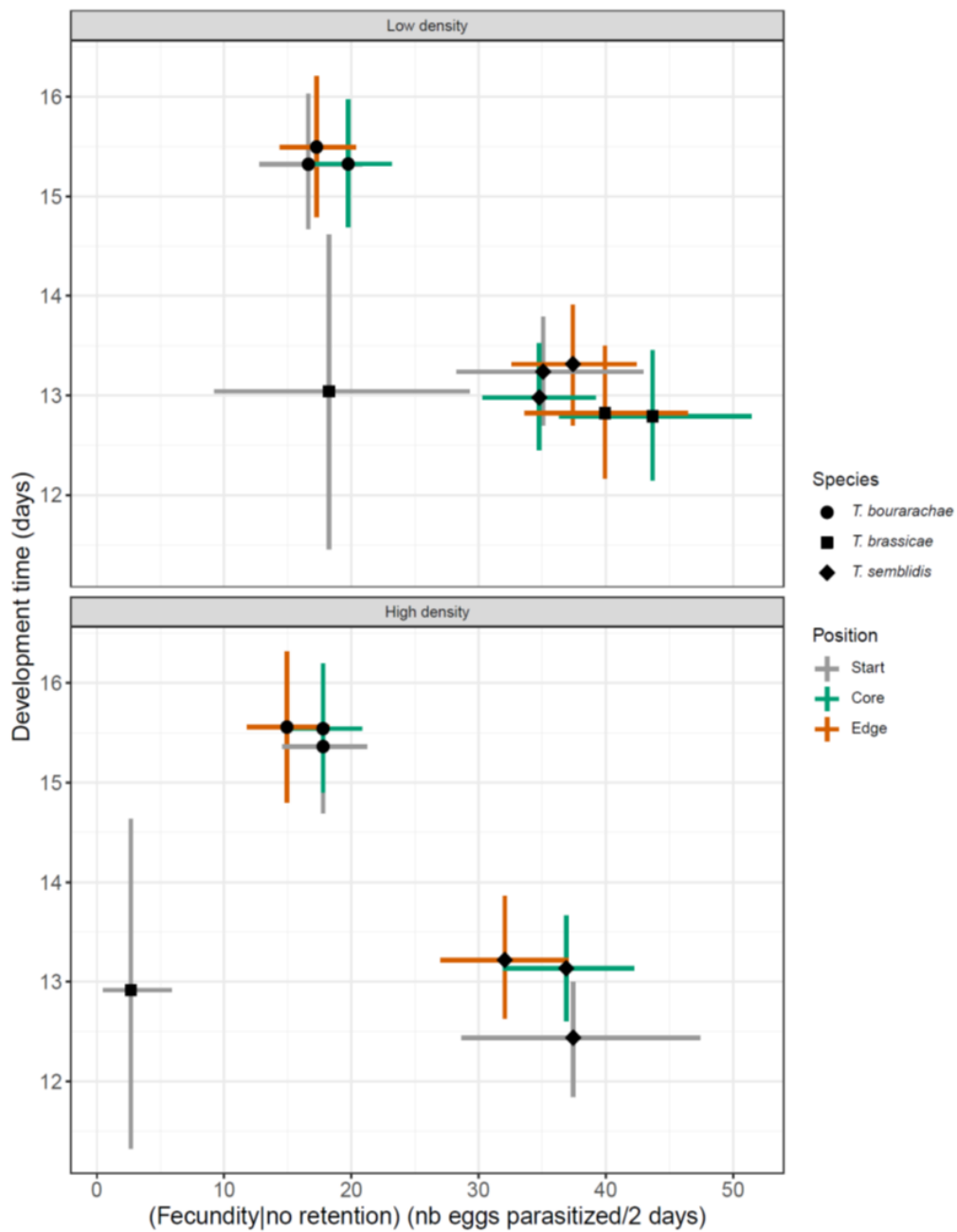


**Supplementary Figure II.2: Landscape-level correlations between phenotypic and demographic traits.**

Random effects intercept for phenotypic traits refers to initial population/low density replicates.

All correlations but one were not significantly different to zero, based on their 95% quantile intercept. The only correlation was between development time at low density in initial populations and the mean effect of core patches in development time (-0.47 [-0.74; -0.12]). It implies that initial landscapes presenting longer development time than expected tends to evolve shorter development times in core patches. This correlation can be related to the protocol, as individuals emerging too late compared to the fixed development time might miss the 2-days window of the experiment. It can be supported by the same (not significant) negative correlation between the same initial population development time and its value in front patches.

## Supplementary Material 4 - Pace-of-life axis



**Supplementary Figure II.3: Posterior development time as a function of fecundity for the two density modalities, species, and locations.**

Each coloured cross represent 95% highest density interval for the two traits plotted along with their means in black, at every species (shape clue) × location (colour clue).

## Supplementary references

Guicharnaud C, Groussier G, Beranger E, Lamy L, Vercken E, Dahirel M (2023) Life-history traits, pace of life and dispersal among and within five species of *Trichogramma* wasps: a comparative analysis. *Peer Community Journal*, **3**: e57. <https://doi.org/10.24072/pcjournal.294>

**To sum up :**

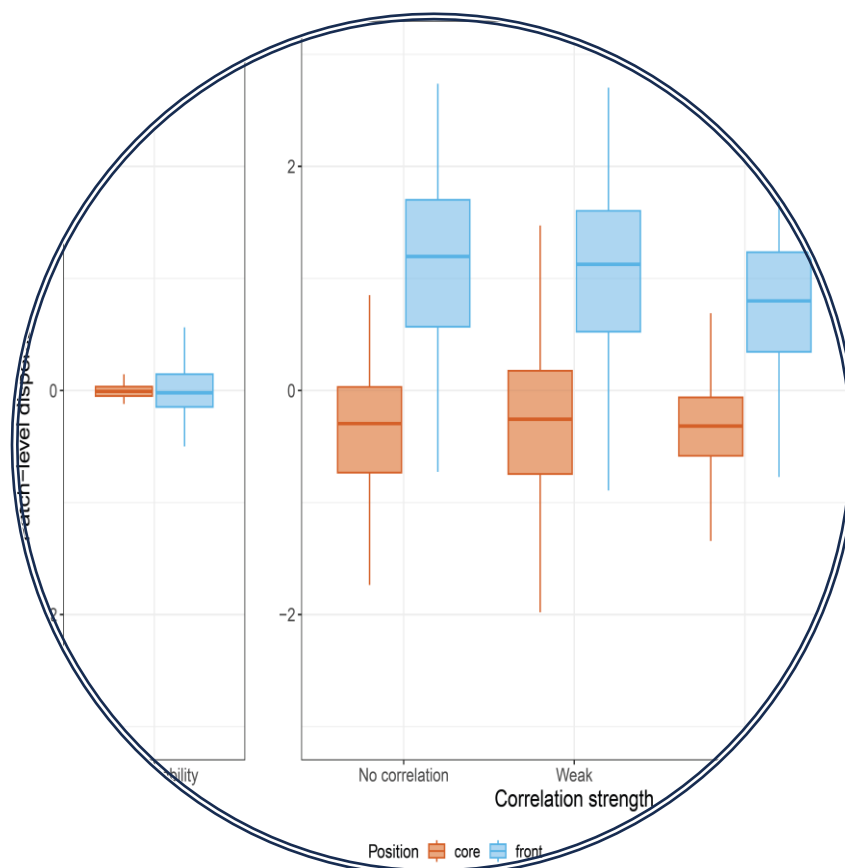
- **An interspecific pace-of-life axis is found at the interspecific level in the five species of *Trichogramma* studied**
- **No correlations between life-history traits and dispersal was found. All species showed similar effective dispersal probabilities**
- **The slowest species, *T. bourarachae*, presented both positive density-dependence in fecundity and dispersal rates.**
- **A potential correlation between the position on the pace of life and pushed/pulled continuum was found in three species of *Trichogramma*.**

### III- Evolution of trait correlation and dispersal traits: does it influence pushed/pulled dynamics?

**Appendix 1: Individual variation in dispersal shapes the fate of pushed vs. pulled range expansions (authors: Maxime Dahirel, Chloé Guicharnaud, Elodie Vercken)**

**Article 3: Competition-colonisation trade-off and dispersal evolution along pushed/pulled expansion dynamics**

*Disclaimer: The article within this chapter is in preparation; The main results are presented alongside basic statistical tests and first elements of discussion.*



## A prologue: Individual variation in dispersal shapes the fate of pushed vs. pulled range expansions

### **Appendix 1 : A quick summary (see Appendix 1 for full text)**

This article has a leading question: How does individual variation in maximum dispersal rate and density-dependent dispersal interact to influence expansion dynamics alongside their position on the pushed/pulled continuum?

We used Individual-Based Models (see below for more information on those models) to simulate expansions with different trait distributions, sources of said variation, or with or without evolution under varying levels of dispersal mortality and low-density fecundity. Key results are presented below, see full text in [Appendix](#) for details.

In the absence of evolution and when mortality was low, classical expectations of pushed/pulled dynamics were met; scenarios with stronger positive density-dependence in dispersal showed higher neutral genetic diversity retention and relative observed velocities.

Dispersal trait evolution, was highly dependent on initial dispersal density-dependence, with higher values of all traits when said density-dependence was positive. Most scenarios led to increased density dependence (therefore more pushed expansions), except when individual fecundity or dispersal mortality were low.

Interestingly, high dispersal costs in the absence of evolution seem to disconnect neutral genetic diversity retention from positive density dependence, where pushed expansion theory (which ignores dispersal mortality) usually posits a strong intrinsic link between the two. Trait evolution restored the positive relationship between density dependence and genetic diversity retention. We assume this is due to evolution causing increases in positive density-dependence.

Overall, this article highlighted the importance of accounting for the environment, such as the dispersal cost, when predicting expansion dynamics. A key finding is that most scenarios led to a shift toward more pushed expansions, contrary to Erm & Phillips (2020)'s results based on Allee effects, demonstrating a possible variation in expectations based on which mechanism generated pushed expansions.

## Individual-Based Models

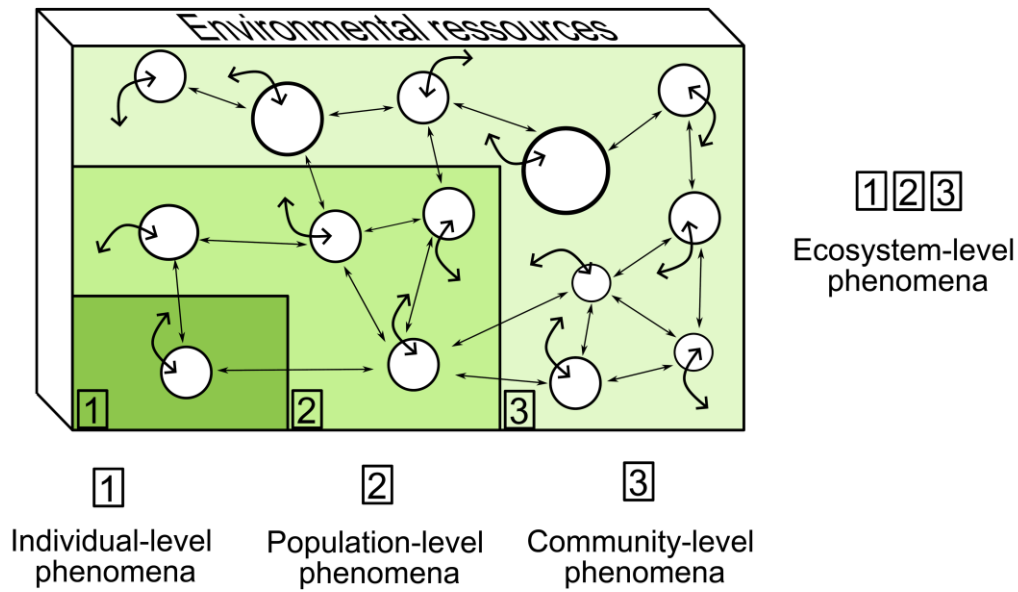
Individual-Based Models (IBMs), also known as Individual-Oriented (Hogeweg & Hesper, 1990) or Agent-Based (Bonabeau, 2002) Models, use individuals (or agents) as the basic unit of the models. IBMs allow for the explicit integration of variations between individuals (or agents), with different rules depending on the individual environment and its interactions with other individuals (Huston et al., 1988; DeAngelis & Grimm, 2014). In the review of Grimm et al. (2005), the authors open with an interesting comparison about the discrete nature of agents within such models: "What makes James Bond an agent? He has a clear goal, he is autonomous in his decisions about achieving the goal, and he adapts these decisions to his rapidly changing situation". On top of allowing the inclusion of discrete and variable individual units, IBMs can present simpler implementations of complex phenomena as long as it can be reduced to individual rules. This advantage is the main reason why IBMs are prevalent in fields where individual-level rules and sources of stochasticity are well understood, but the overall resulting dynamic is too complex, and potentially too stochastic, to be represented by one population-level equation (i.e. DeAngelis & Mooij, 2005; Axtell & Farmer, 2022).

IBMs can be used in many fields, such as economics (reviewed in Axtell & Farmer, 2022), molecular dynamics (Troisi et al., 2005), oncology (Wang et al., 2015), and was quickly applied in ecology (Huston et al., 1988; DeAngelis & Grimm, 2014; Railsback & Grimm, 2019), as it permits to integrate two critical aspects of biology, lacking in other mathematical models: unique individuals and localisation of interactions (Huston et al., 1988). Variations in traits among individuals are important for evolutionary processes, and one individual can only perceive and interact with the direct biotic or abiotic environment. IBMs are a bottom-up complementary approach to other top-down ecological modelling, such as differential equation population models, which exhibit population-level concepts and averaged individual properties (Grimm, 1999).

This bottom-up approach also allows for emerging properties at higher levels than the individuals (**Figure III.1**), which is useful when the study's goal is to understand how self-organisation and global patterns could rise from autonomous and discrete entities under specific conditions (reviewed in Breckling et al., 2005, 2006; Reuter et al., 2005). This



combination of individual variability and potentiality for emerging population-level patterns made IBMs excellent for our study; it will allow us to observe how the presence of individual variability in negative trait correlation and dispersal traits could influence a population-level expansion, its evolutionary trajectories, the stochastic processes such as genetic drift, and pushed/pulled dynamics.



**Figure III.1: Graphical conceptualisation of an Individual-Based Model illustrating how individual-level processes can produce patterns at higher levels of complexity.**

Individuals are represented by white circles and species by different circle sizes. The environmental resources can be modelled as either homogeneous (similar to this graphic) or with space and/or time variations. These resources influence and are influenced by individuals within different species in a community (curved arrows), which in turn can indirectly affect other individuals. Individuals or species also interact directly with each other (straight arrows). Population-level rules (1) can result in population-level phenomena (2), such as intraspecific competition or spatial expansions in our case. It can also lead to community-level phenomena (3) with interspecific competition or trophic structures. All levels connect and aggregate together to generate ecosystem-level phenomena (1,2,3) (nutrient cycle, total productivity, energy flux, stability and resilience...). Modified from Huston et al. (1988).

## Article 3: Competition-colonisation trade-off and dispersal evolution along pushed/pulled expansion dynamics

Chloé Guicharnaud, Elodie Vercken, Maxime Dahirel

### Introduction

Understanding the mechanisms behind population expansion inside a new habitat has recently been the subject of increased scrutiny. This scrutiny is a result of increased awareness about how population range shifts caused by climate change (Rockwell-Postel et al., 2020; Rubenstein et al., 2023) or human-made biological invasion (Myers & Bazely, 2003; Pyšek et al., 2010) can have cascading effects on local communities and transform ecosystems.

We can analyse the mechanisms behind biological expansions by observing current or previous expansions in the wild (Walter et al., 2020; Scordo et al., 2023; Ewers et al., 2023), but it may often be easier to recreate and analyse either experimental expansions in controlled conditions or simulated populations. Experiments in controlled conditions allow researchers the possibility to tailor the environment to specific questions (Williams & Levine, 2018; Dahirel, Bertin, Calcagno, et al., 2021) and to modify or cancel biological processes (Van Petegem et al., 2018). It allows us to see how they will impact the overall expansion process of their biological model, which is rarely possible to do in nature. However, even experiments have their limits (be it money, time, space, or uncontrollable parameters).

These experimental limits can be circumvented further by using various modelling methods. Models allow us to precisely change the parameters or underlying mechanisms of interest without interferences by other mechanisms that could lead to incorrect interpretations (Cooper, 2003; Peck, 2004). Researchers have extensively used models to study expansion dynamics (Urquhart & Williams, 2021; Morel-Journel et al., 2023; Zhu et al., 2023), including in many cases Individual (or Agent) Based Models (Travis et al., 2009; Dominguez Almela et al., 2020). IBMs model the behaviour of individuals using simple

rules, and how these individuals interact may lead to emergent population-level properties that are not predictable from simple mathematical modelling, increasing realism (DeAngelis & Grimm, 2014; Railsback & Grimm, 2019). Those models allow for variation in traits between individuals, a cornerstone of evolutionary processes, that is highly to take into account during expansions, as explored by Griffith & Watson (2006), Jongejans et al. (2011), Peischl et al. (2015) or reviewed in Williams et al. (2019) and Miller et al. (2020). Ecological dynamics may influence both deterministic and stochastic evolutionary processes; expansion fronts are spatial situations in that they create relatively stable and predictable spatial gradients in population density, which may alter expected evolutionary dynamics compared to stationary populations (Rice et al., 2013; Gruber et al., 2017).

When studying trait evolution, our expectations may change when we consider the possibility for multiple traits to be correlated and, therefore, co-evolve. Many such studies in expansion contexts have focused on the effect of a density-independent dispersal-fecundity trade-off (Hughes et al., 2003; Ochocki et al., 2020; Urquhart & Williams, 2021). Such trade-off should lower the expansion velocity, as the energy allocated to dispersal has to be balanced with the allocation for reproduction (Deforet et al., 2019; Marculis et al., 2020). This focus is understandable for two reasons: first, this is a common trade-off in nature (Gu et al., 2006; Karlsson & Johansson, 2008; Guerra, 2011; Duthie et al., 2015), so knowing how it can influence range front dynamics can offer essential insights for managing expanding species (Shea et al., 2010). Second, low-density population growth and dispersal rates are the only two parameters needed to accurately predict expansion velocity in many situation (Stokes, 1976; Lewis & Kareiva, 1993; Kot et al., 1996).

However, those studies ignore density dependence in either growth or dispersal traits and how it can influence expansion characteristics. So-called "pulled" expansions are the "classical" ones described by many of the models mentioned above, in which velocity is determined only by growth and dispersal at low density, i.e. at the very edge of the expansions. On the other hand, when dynamics are instead driven by larger populations farther behind the range edge, thanks to positive density-dependence on growth (Allee effect) and/or dispersal, this leads to "pushed" expansions where classical models based on pulled dynamics cannot accurately predict dynamics (Stokes, 1976; Birzu et al., 2018;

Gandhi et al., 2019). Pushed expansions tend to have higher genetic diversity and reduced genetic drift along the front (Roques et al., 2012; Bonnefon et al., 2014) and higher expansion velocity compared to a pulled expansion with similar growth and dispersal values at low densities (Birzu et al., 2018).

There is evidence that density-dependence can reshape the way trait combinations (including dispersal) are distributed at high vs low density (Clark et al., 2022), meaning there is the potential for complex interactions between the evolutionary effects of pushed-pulled dynamics (driven by density-dependence) and traits correlations (including trade-offs) during expansions. We do note that another highly studied trade-off during expansion, the competition-colonisation trade-off (where good colonising species or individuals are poor inter- or intra-specific competitors; (Skellam, 1951; Levins & Culver, 1971; Yu & Wilson, 2001; Calcagno et al., 2006; Wetherington et al., 2022), does include density-dependence at least implicitly. However, there have been so far no actual connections made between the presence of trait correlations or trade-offs and expansion "pushedness".

We explore here how incorporating more realism on life-history traits through the presence of a negative correlation can further shape our expectations. We build this paper on our previous works showing that individual variation and evolution in dispersal density-dependence could alter the predictions of classical pushed/pulled theory ([Appendix 1](#)), especially regarding the link between initial density-dependent dispersal and genetic diversity. When dispersal traits were allowed to evolve, the positive link between initial density-dependent dispersal and genetic diversity was maintained even at low fecundity and high dispersal costs but also showed higher genetic diversity for identical initial values than when there was no evolution possible for most trait combinations. Although very detailed models describing trait correlations exist (e.g. Wright et al., 2019), we start here with a much simpler first exploration of how trait correlations may shape pushedness; the underlying modelling approach can and will be expanded to further trait correlations.

Our main goal here is to see how adding a simple life-history trade-off between adult fecundity and juvenile survival (which are both expected to be shaped by density) can affect key characteristics of pushed vs. pulled expansions: neutral genetic diversity on one

hand and key dispersal traits (strength of density-dependence and low-density dispersal rate) on the other. For that, we generated replicated simulated expansions with various trait correlation strengths and density-dependence in dispersal and measured genetic diversity and dispersal traits after expansion. We will work with three predictions:

- In absence of trait correlation, the general prediction is that an initial positive density dependence should result in (more) pushed expansion, leading to the maintenance of a higher genetic diversity at the expansion front (Roques et al., 2012; Bonnefon et al., 2013, 2014).
- When the correlation strength increases, low competitors should benefit from seeking less dense habitats (Wright et al., 2020), leading to higher dispersal, at least at medium or low densities, and stronger density-dependence in dispersal.
- Through this increase of density-dependent dispersal at the edge, leading to more pushed expansions, the presence of trait correlation should result in higher neutral genetic diversity.

## Material and methods

### *Simulations description*

#### General setup

We wrote an Individual-Based Model using NetLogo (Wilensky, 1999) version 6.2 where haploid and asexual individuals disperse along a 1-dimensional landscape. Both time and space are discrete, and generations are non-overlapping. Each discrete space is called a patch and shares the same carrying capacity,  $K$ . They are spatially differentiated by their position, starting from  $x = 0$  as the far-left side of the landscape.

The goal is to observe how the presence of a negative trait correlation and the evolution of dispersal and life-history traits may affect the relation between density-dependent dispersal and genetic diversity, using three metrics linked to density-dependent dispersal and neutral genetic diversity. The model simulates fecundity, juvenile survival, and dispersal dynamics, all incorporating stochasticity and individual variation. Dispersal is to

the nearest patches only. Individuals possess four traits, and individual variation can either be perfectly heritable from parent to offspring or randomised every generation:

- $z_1$ , representing the individual deviation from the average reproductive potential at low densities,
- $z_2$  representing individual variation in juvenile survival at high densities ( $= K$ ),
- $\text{logit}(d_0)$ , the logit of the expected dispersal rate at low density, using the average dispersal rate at density 0  $disp$  to draw initial individuals' values (see Table III-1),
- And  $\beta$  the slope of the relationship between dispersal rates and density (on the logit scale), using the initial density-dependent slope parameter slope for initial individuals' values.

As a key point of the differences between pushed and pulled expansions is neutral genetic diversity, individuals also vary at a neutral locus  $Loc$  with two possible allelic values (0 or 1). Individuals also possess a lineage identifier,  $LineageID$ , which denotes which of the initially released individuals they originate from. The potential correlation between  $z_1$  and  $z_2$  can be defined through an initial correlation value  $r$ .

#### Model initialisation and life cycle

The model starts by introducing  $K$  individuals at the far-left patch (position  $x = 0$ ). Those individuals are all adults that haven't dispersed or reproduced yet. Initial  $z_1$  and  $z_2$  were drawn from a Bivariate Normal distribution  $N\left(\begin{pmatrix} 0 \\ 0 \end{pmatrix}, \begin{pmatrix} \sigma_{z1}^2 & r\sigma_{z1}\sigma_{z2} \\ r\sigma_{z1}\sigma_{z2} & \sigma_{z2}^2 \end{pmatrix}\right)$ , with standard deviations equal to  $\sigma_{z1} = 1$  and  $\sigma_{z2} = 1$ . As bivariate Normal distributions are not implemented in base Netlogo, we used existing formulas to generate properly correlated random draws for both *traits* (e.g. Tong, 1990).  $\text{logit}(d_0)$  and  $\beta$  were drawn from separate Normal distribution  $N(disp, \sigma_{\text{logit}(d_0)}^2)$  and  $N(slope, \sigma_{\beta}^2)$ . Both standard deviations were fixed at 1. Initial individuals are also assigned one of the two possible  $Loc$  allelic values at random and a unique  $LineageID$  number (a number ranging from 1 to  $K$ ). After this setup, the model starts its cycle, similar for every generation:

- The population size  $N$  of each patch is checked, and patch-level summaries are collected: mean and variance of traits, the frequencies of the two alleles at the neutral locus  $Loc$  and the numbers of remaining lineages.
- Adults enter a dispersal phase. The probability to disperse follows a 2-parameter sigmoidal function, similar to how empirical dispersal data are analysed with generalised linear models (e.g. Szűcs et al., 2017). Dispersal is Bernoulli-distributed, with the individual dispersal probability being  $D = \text{logit}^{-1}(\text{logit}(d_0) + \beta \times (\frac{N}{K}))$ . Individuals that disperse move to one of the nearby patches at random.
- Population sizes  $N$  are updated after dispersal.
- Adults reproduce. The number of juvenile offspring per individual is drawn from  $\text{Poisson}(\lambda)$ , with the mean derived from a Ricker function:  $\lambda = e^{(r_0 + z_1)(1 - (\frac{N}{K}))}$ .  $r_0$  is the baseline low-density growth rate and is a global parameter fixed for each expansion, with  $z_1$  used separately to model individual variation. Juveniles inherit their parent  $Loc$  allele and  $lineageID$ ; all four traits  $z_1$ ,  $z_2$ ,  $\text{logit}(d_0)$  and  $\beta$  are either inherited directly in the same way (if trait evolution) or redrawn at random following the same rules as in the initial generation (if no trait evolution).
- All adults die.
- Patch population sizes are again updated.
- Juveniles enter a survival phase. Juvenile survival is Bernoulli-distributed, with individual juvenile survival probability being density-dependent as follows:  $S = e^{(-a \times (\frac{N}{K}))}$  (e.g. Bocedi et al., 2021) where the decay rate  $a$  can be rewritten as  $a = \log(\frac{1}{s_k})$ , where  $s_k$  is the individual expected survival rate when  $N = K$ :  $s_k = \text{logit}^{-1}(\text{logit}(survival) + z_2)$ , with survival being the baseline juvenile survival rate at  $N = K$ . and  $z_2$  as the individual variation.
- Surviving juveniles become adults.

### Initial parameters

We created simulations according to all possible combinations of starting parameters presented in [Table III-1](#), with 100 replicates per combination for a total of 1200 simulated

expansions. We used the *nrx* package (Salecker et al., 2019) in R version 4.3.0 (R Core Team, 2023) to run our Netlogo simulations for 100 generations (or until they went fully extinct). This number of generations was arbitrarily chosen based on previous similar simulations ([Appendix 1](#)) and confirmed by graphical observation of trait evolution during preliminary runs.

Initial dispersal trait values were chosen so that low-density dispersal rates are realistically close to the literature (e.g. Stevens et al., 2013; Fronhofer et al., 2018) and that, in the absence of phenotypic variation, dispersal rates roughly double between  $N = 0$  and  $N = K$  when dispersal is density-dependent.

**Table III-1: Simulation parameter values chosen in our different simulation sets.**

All combinations of parameters are examined.

Parameters	Description	Values
$h^2$	Initial trait heritability: only 0 (traits are reshuffled each generation) or 1 ( traits are perfectly inherited) are allowed	0 ; 1
<i>slope</i>	Initial strength of density-dependent dispersal	0 ; 1
$r$	Juvenile survival/adult reproduction correlation	-1 ; -0.5 ; 0
<i>disp</i>	Average dispersal rates at density 0	0.2
$r_0$	Baseline low-density growth rate	Log(4)
<i>survival</i>	Average juvenile survival at density K	0.5
$K$	Patches carrying capacity and the maximum number of unique lineages	500

### Analyses

As the dynamics of genetic diversity are one of the main differences between pushed and pulled expansions (Roques et al., 2012; Bonnefon et al., 2014), we analysed two metrics linked to the maintenance of genetic diversity in space and time, respectively.



First, we divided individuals in an expansion into two fractions based on the neutral allele they bear at *Loc*. We used the ratio between the expansion speeds of the lagging fraction and the whole front to measure genetic diversity in space ([Appendix 1](#)). The closer this metric is to 1, the more the lagging allele is near the farthest patch at the front edge, which implies a higher spatial neutral genetic diversity along the expansion. We examined this metric at the last generation only.

Second, for each generation  $t$ , we collected the number of unique *LineageID* remaining in the range core ( $x = 0$ ) and in the farthest patch at the front edge of the expansion. For each of these patches at each replicate, we assumed that this number decayed with time following a power law:  $y = 1 + (K - 1) \times t^{-\alpha}$ . We estimated its parameters using Nonlinear Least Squares estimations. We then used the power law exponent  $\alpha$  as a measure of neutral genetic diversity loss in time, with the expectation that this loss is more substantial (higher alpha) at the edge than the core. In pushed contexts, there should be a lower decay rate at the edge, meaning that the ratio between edge and core decay rates  $\alpha_{edge}/\alpha_{core}$  should also be lower. We used this ratio as a second metric of genetic diversity.

Using linear models and ANOVAs, we compared these metrics between expansions that varied in the presence/absence of evolution, the initial average density-dependence of dispersal, the intensity of the life-history correlation, and possible interaction effects. More precisely, as a fundamental aspect of pushed dynamics is density dependence, we use here as responses the differences between initial density-dependence ( $\beta = 1$ ) and no density-dependence ( $\beta = 0$ ) as a function of the different treatments (heritability and correlation strength). To estimate these differences, density-dependent and density-independent replicates that were identical in all other starting conditions (parameters in [Table III-1](#) and initial random seed) were matched. To evaluate whether the overall differences between density-dependent and density-independent (irrespective of correlations or heritability) were different from 0, we fit additional intercept-only linear models, and determine whether these intercepts were different from 0. Detailed measures of allelic retention and decay rates for each treatment and position separately, rather than these differences, are presented in [Supplementary Figure III.1](#) and [Supplementary Figure III.2](#).

We additionally looked at how dispersal traits ( $\beta$  or  $d_0$ ) may have evolved in core and edge patches during simulations and how that evolution could have been affected by a negative trait correlation. We expected to find a variation in density-dependent selection between the range core and expansion edge, so we analysed them separately. We fit linear models and used ANOVAs to compare dispersal traits values at the range core and at the edge between scenarios varying in their trait correlation strength or heritability. Another linear model and ANOVA was used to analyse the effect of position along the expansions (core or edge) for replicates with inherited traits only. Detailed measures are presented in [Supplementary Figure III.3](#) and [Supplementary Figure III.4](#).

As a check on the validity of our model, we present [Supplementary Figure III.5](#) and [Supplementary Figure III.6](#) results on the dynamics of the life-history traits  $z_1$  and  $z_2$ : based on the competition-colonisation theory (Levins & Culver, 1971; Turnbull et al., 2004), we expect higher values of juvenile survival at high density at the range core, and higher values of adult reproduction at low density in the expansion edge (Orlando et al., 2013), with more contrasted values of the opposed variable for each position as the strength of the (negative) correlation between the two increases.

## Results

### Neutral genetic diversity for various levels of trait correlation and initial density-dependent dispersal

The presence of density-dependence in dispersal resulted in a higher conservation of genetic diversity after 50 generations of expansion, both when considering its spatial (p-value < 0.001) or temporal (p-value < 0.001) component. However, the conservation of neutral genetic diversity in space was not influenced by trait heritability, trait correlation, or their interaction (p-value<sub>heritability</sub> = 0.347, p-value<sub>correlation</sub> = 0.772, p-value<sub>interaction</sub> = 0.735) ([Figure III.2](#)). In contrast, heritability did influence the conservation of diversity in time (p-value = 0.015), with slightly higher ratios of the decay rates when traits are inherited ([Figure III.3](#)). Trait correlation, or the interaction between correlation strength and heritability, had no effect on the temporal dynamics of neutral diversity (p-value<sub>heritability</sub> = 0.192 ; p-value<sub>interaction</sub> = 0.302).

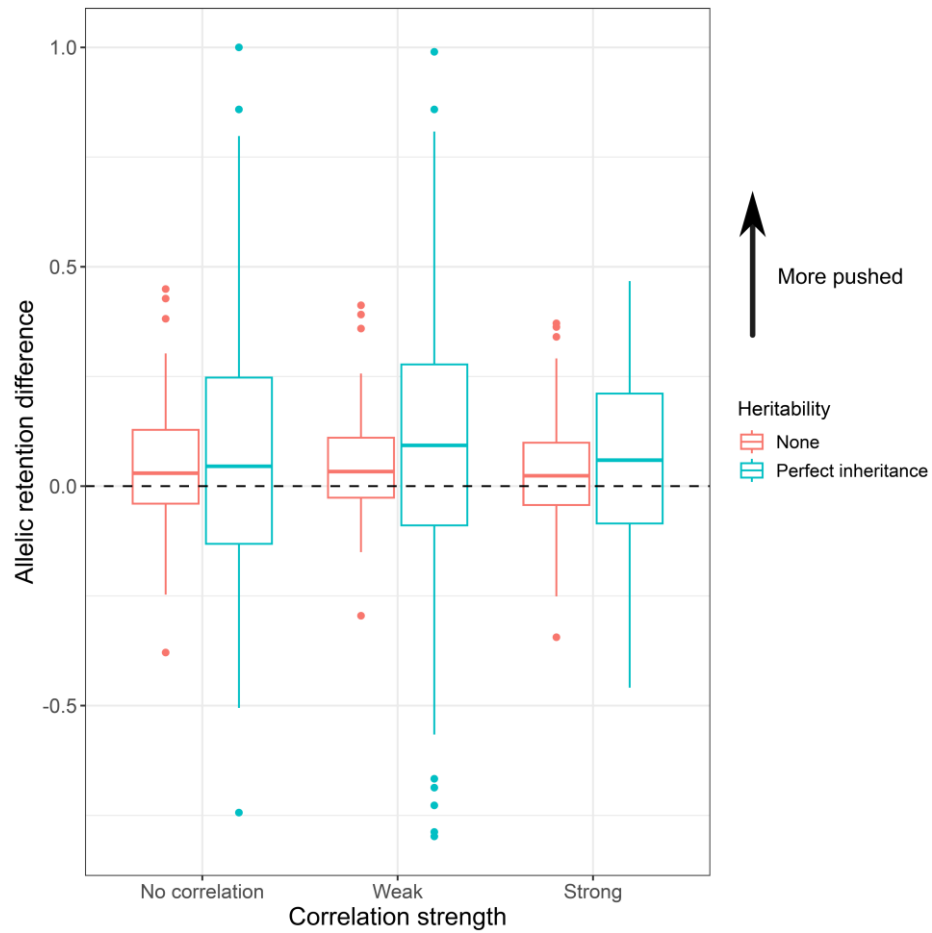
## Evolution of dispersal traits at core and edge ranges

Dispersal evolution (both in slope and low-density dispersal) proceeded in qualitatively and quantitatively similar ways whether the density-dependent dispersal was high or low, therefore we present only results on expansions with initial mean  $\beta = 0$ , for simplicity. Complete results are presented in [Supplementary Figure III.3](#) and [Supplementary Figure III.4](#).

As expected, we observed no significant deviation from initial dispersal trait values when traits were not heritable ([Figure III.4](#), [Figure III.5](#) left) and a significant effect of heritability on trait evolution ( $p < 0.001$ ) ([Figure III.4](#), [Figure III.5](#) right). Allowing evolution led to consistently higher values of both  $d_0$  and  $\beta$  at the range front, compared to starting values ([Figure III.4](#), [Figure III.5](#)), while in the core patches, the density dependence always decreased and ([Figure III.4](#)) (it even became negative in case of no initial density dependence but it mainly stayed positive otherwise; see [Supplementary Figure III.3](#)).

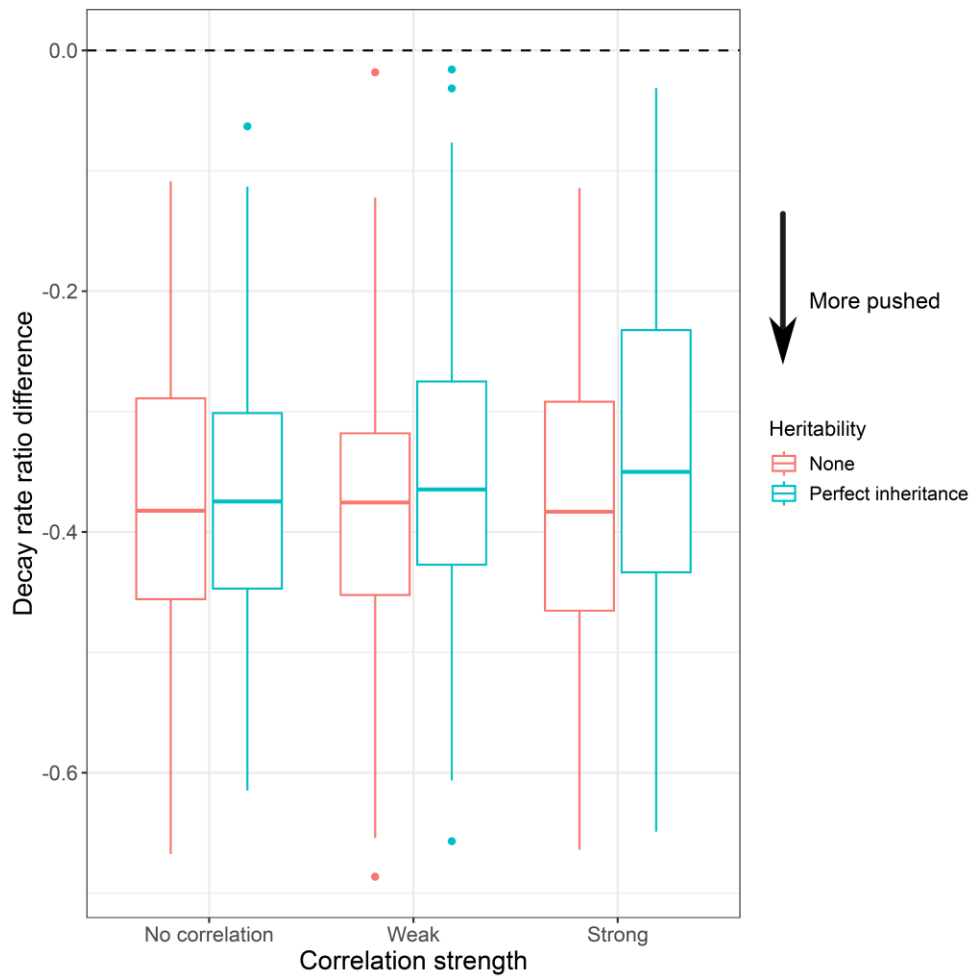
Negative life-history traits correlations did not affect the evolution of density-dependence ( $\beta$ ) mean values, whether at the range core or the edge ( $p = 0.613$  and  $0.078$ , respectively; [Figure III.4](#)), with also no evidence of an interaction between initial correlation and heritability either way ( $p = 0.651$  in the range core and  $p = 0.303$  in the edge).

The dispersal rate at low density presented significant variations as a function of correlation strength but only at the expansion edge ( $p\text{-value}_{\text{core}} = 0.282$ ,  $p\text{-value}_{\text{edge}} = 0.002$ ) with increasing values at the front edge ([Figure III.5](#)), meaning that for a similar number of generations, a strong negative correlation in life-history traits seems to allow a quicker increase of dispersal rates at a low density in the edge patch. The interaction between heritability and correlation strength was also significant only at the edge ( $p\text{-value}_{\text{core}} = 0.474$ ,  $p\text{-value}_{\text{edge}} = 0.018$ ).



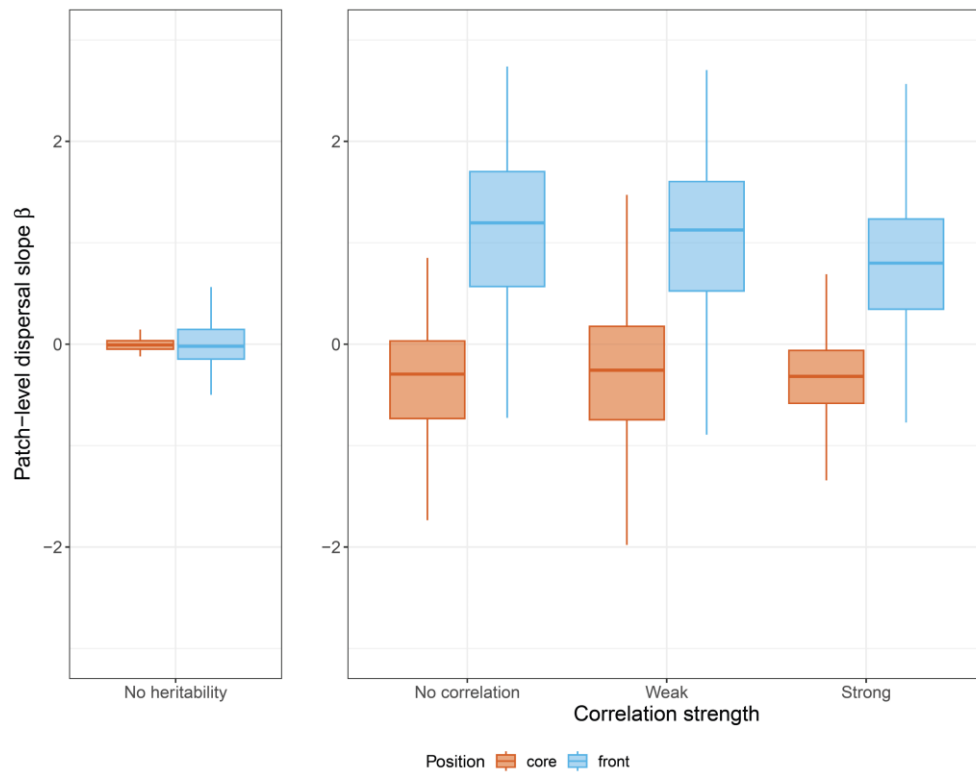
**Figure III.2: Plot of neutral alleles retention difference between treatments with and without initial density-dependent dispersal for three levels of correlation strength.**

The dotted line corresponds to an absence of difference between the two levels of initial density-dependence. Bars represent the 95% highest density interval, while coloured points are the mean value of the difference. The arrow represents the direction trait values should take to imply more pushed expansions.

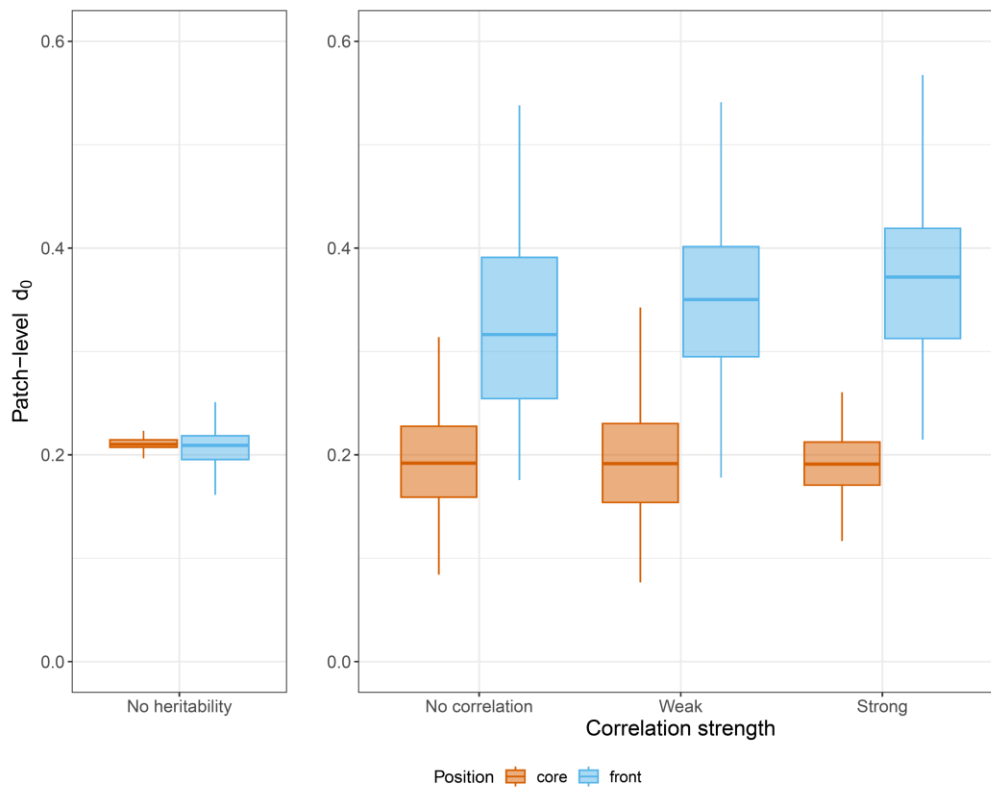


**Figure III.3: Plot of the decay rate ratio difference between treatments with and without initial density-dependent dispersal for three levels of correlation strength.**

The ratio is obtained by dividing the range edge decay rate by its value at the range core. The dotted line corresponds to an absence of difference between the two levels of initial density-dependence. Bars represent the 95% highest density interval, while coloured points are the mean value of the difference. The arrow represents the direction trait values should take to imply more pushed expansions.



**Figure III.4: Mean dispersal slope (density-dependence strength) value in range core and front edge as a function of correlation strength for an initial slope of 0.** Boxplots represent the median, 25th and 75th percentiles.



**Figure III.5: Mean dispersal rate at low density in range core and front edge as a function of correlation strength for an initial slope of 0.**

Boxplots represent the median, 25th and 75th percentiles.

## Discussion

*Model confirmation: Initial positive density-dependence generate more pushed expansions and competition/reproduction sorting*

We presented a first exploration of the way trait correlations could alter pushed/pulled dynamics. While our model was simple, it presented various expected behaviours regarding e.g. the spatial sorting of good colonisers at the range edge (Higher  $z_1$  values compared to the range core when a negative correlation with  $z_2$  is present) and good competitors at range core (Higher  $z_2$ ) ([Supplementary Figure III.5](#), [Supplementary Figure III.6](#)).

We can observe a global effect of initial positive density-dependent dispersal in both of our metrics of neutral genetic diversity ([Figure III.2](#), [Figure III.3](#)). This later sign of higher

neutral genetic diversity follows previous studies linking positive density-dependence in dispersal with pushedness (Birzu et al., 2019; Dahirel, Bertin, Haond, et al., 2021; Haond et al., 2021). Those results complete studies historically more focused on the importance of positive density-dependence in reproduction, or the Allee effect, in expansion pushedness (Roques et al., 2012; Bonnefon et al., 2014; Erm & Phillips, 2020). Combining both mechanisms allows for a global view of how positive-density-dependence and its evolution shape expansion dynamics.

Interestingly, while initial positive density-dependence in dispersal significantly affects the two metrics' means, lineage decay rates seem much more influenced (**Figure III.3**) than allele retention (**Figure III.2**). One possibility to explain these differences is that dispersal evolution is more or less strong depending on where patches are located: dispersal density dependence tends to stay positive at the edge only, while its value decreases and can even become negative at the range core (**Figure III.4**) and front edges present higher dispersal rate at low density (**Figure III.5**), correlating with previous studies results (Travis et al., 2009; Weiss-Lehman et al., 2017). While our temporal metric is directly impacted by looking at the lineage decay rate in the furthest front patch, where density-dependent dispersal is the highest, neutral allele retention might be more influenced by values found at the position where the lagging allele is present. This position can be a transition zone between the opposite range core and edge, therefore less subjected to extreme dispersal values.

*Evolution leads to higher dispersal at the edge with a small effect of trait correlation strength for dispersal rates.*

When looking at the evolution of dispersal trait values between range core and edge, we can see that front patches always present higher dispersal density dependence and dispersal rates at low density, no matter the correlation strength. In the absence of correlation, these results can be explained by the effect of spatial sorting, where good dispersers end up at the range edge (Phillips & Perkins, 2019). Individuals with positive dispersal slope also tend to disperse more as density increases, like at range core, leading to this slope distribution along the density gradient. Furthermore, an increase in negative trait correlation strength between juvenile survival and adult fecundity seems to increase



the divergence between range core and edge low-density dispersal rate values; it seems to be primarily driven by a significant effect of the correlation strength on values at the edge (**Figure III.5**). While further analyses are needed, there is the possibility that at the range edge, the increased negative correlation strength and spatial sorting results in populations of very good reproducers but also very bad competitors and that an increased dispersal rate, even at low densities would allow for a quick (and preemptive?) escape to conspecific pressures (Wright et al., 2019). As for an absence of significant effects of trait correlation on the dispersal slope evolution at the edge, while it can be the beginning of a less marked pattern, it is also probable that there is not enough evolutionary pressure on this trait as the increased dispersal rates already resolve the issue of high conspecific density.

If we consider that the absolute strength of density-dependent dispersal is a meaningful estimator of the position on the pushed/pulled continuum (following Birzu et al., 2018, 2019; **Appendix 1**), then our results suggest that expansions tend to get more pushed when traits are heritable, which confirms results in **Appendix 1**, and goes the opposite way than Erm & Phillips (2020). While we observed the increase in dispersal rates as predicted by theory (Travis et al., 2009), we did not have an evolution toward density independence at the leading edge, even though it was observed on experimental expansions (Weiss-Lehman et al., 2017; Fronhofer et al., 2017) (due to the dispersal rate at low density already high, individuals at range edge keep establishing in empty patches and there is no pressure from high densities). A negative trait correlation does not seem to influence expansion pushedness, still ending more pushed, but further sensitivity analyses will determine if the lower dispersal slope at strong correlations is a result of stochasticity or if our parameter values were not variable or extreme enough to get significant results.

#### *An absence of trait correlation's influence on neutral genetic diversity*

Our last prediction was that the strength of trait correlation should indirectly influence the neutral genetic diversity by increasing the positive density-dependence in dispersal, generating more pushed expansions, therefore allowing neutral genetic diversity to stay high. As no effect of correlation strength on  $\beta$  was observed (**Figure III.4**), it comes to no

surprise that the more indirect effect of correlation strength on neutral genetic diversity was also non-significant (**Figure III.2, Figure III.3**). This could be a result of too indirect influences blurred by cumulated stochasticity between the two mechanisms. The different time scales between the two processes could also be a reason: Neutral genetic diversity is fixed at the beginning of the expansion and cannot be generated through mutations, meaning that there should be a quick decrease of neutral genetic diversity at the leading edge within the first generations, before evolution could really have an effect on the pushedness of the expansion dynamics.

#### *Further perspectives*

Our results imply that individual variation in positive density-dependent dispersal can lead to more pushed expansions irrespective of the negative correlation between traits. They also show that the two neutral diversity metrics used to determine the pushedness have different sensibilities in our parameter ranges. Positive density-dependent dispersal led to more variations in lineage decay rate, while there were no effects of either negative trait correlation or dispersal slope evolution on neutral allele retention. Looking at the value of dispersal slope at the last generation, we can see that trait correlation does not alter the evolution toward lower slope values at the range core and higher density dependence values at the edge (**Figure III.4**). By looking at all the differences in our three metrics (allelic retention, lineage decay rate and dispersal slope), we can see that predicting the position of an expansion within a pushed/pulled continuum is not as easy as expected from biological populations where many interactions and feedbacks may add noise or alter predictions.

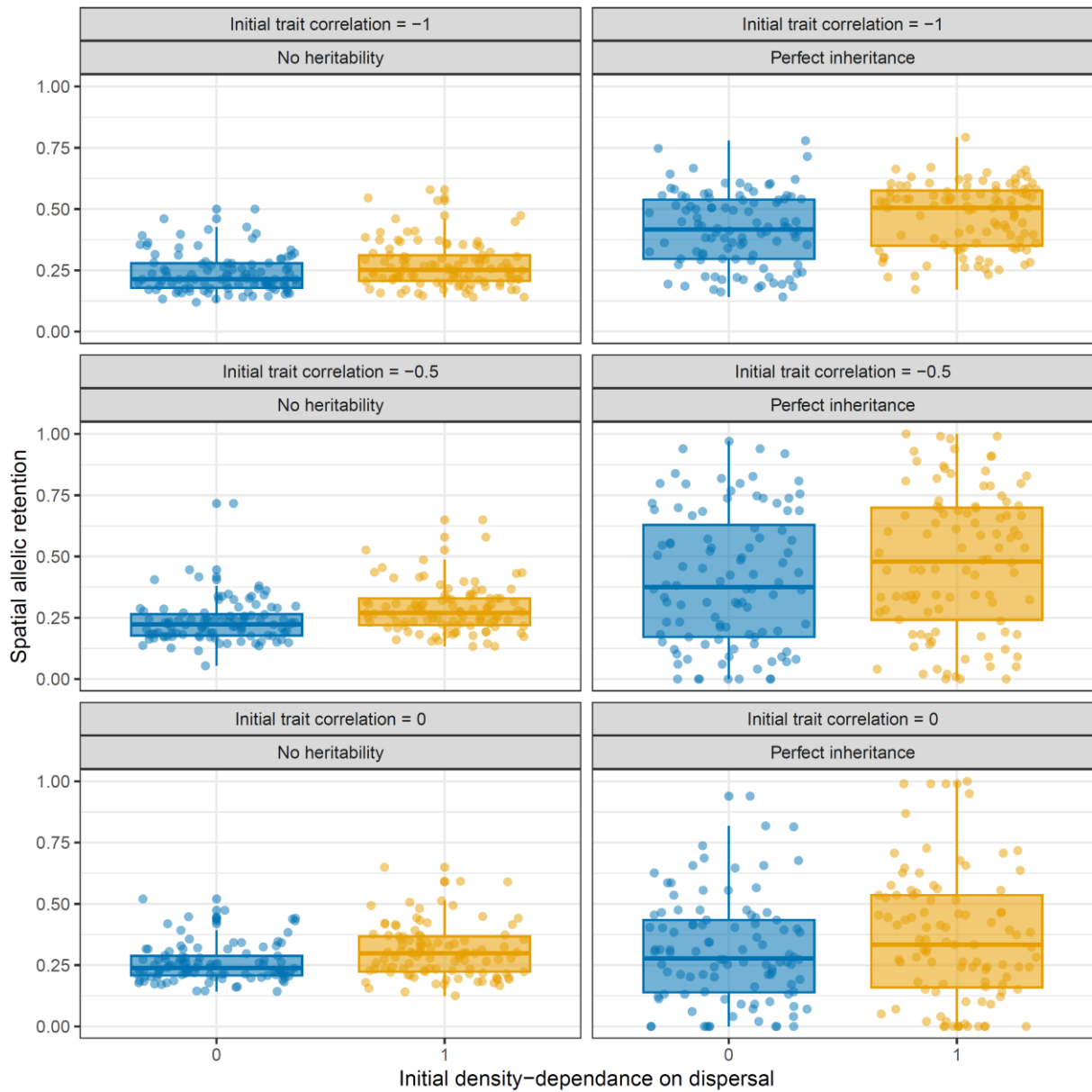
Further analyses, such as studying emerging correlations between traits, are considered and can help us shed some light on some observations. Understanding how and when new patterns emerge is also something to remember when working on experimental expansions or making estimations based on initial values alone. Also, a more precise understanding of density-dependent dispersal patterns along expansions will be able to confirm or not some of our hypotheses concerning neutral allele retention. Building on the influence of trait correlation, we could add a dispersal-fecundity trade-off in later models to see how our results change when dispersal is directly linked to life-history traits.

Finally, sensitivity analyses on key traits such as global reproductive output, global juvenile survival or low-density dispersal, and  $K$  can give us a more precise interpretation. By observing how our result can vary depending on the imputed values of our model could help us determine if our results are scenario-dependent, and different trait values generate different results from our reference case, adding nuance to our discussion. Incorporating dispersal mortality in our simulations is another possibility, as it does have a significant impact in [Appendix 1](#), and observing expansion dynamics for various positions on a pace-of-life axis (simplified by analysing different combinations of juvenile survival and growth rates can loop back on previous experimental expansion studies (see [Chapter I](#))).

## Article 3: Supplementary Materials

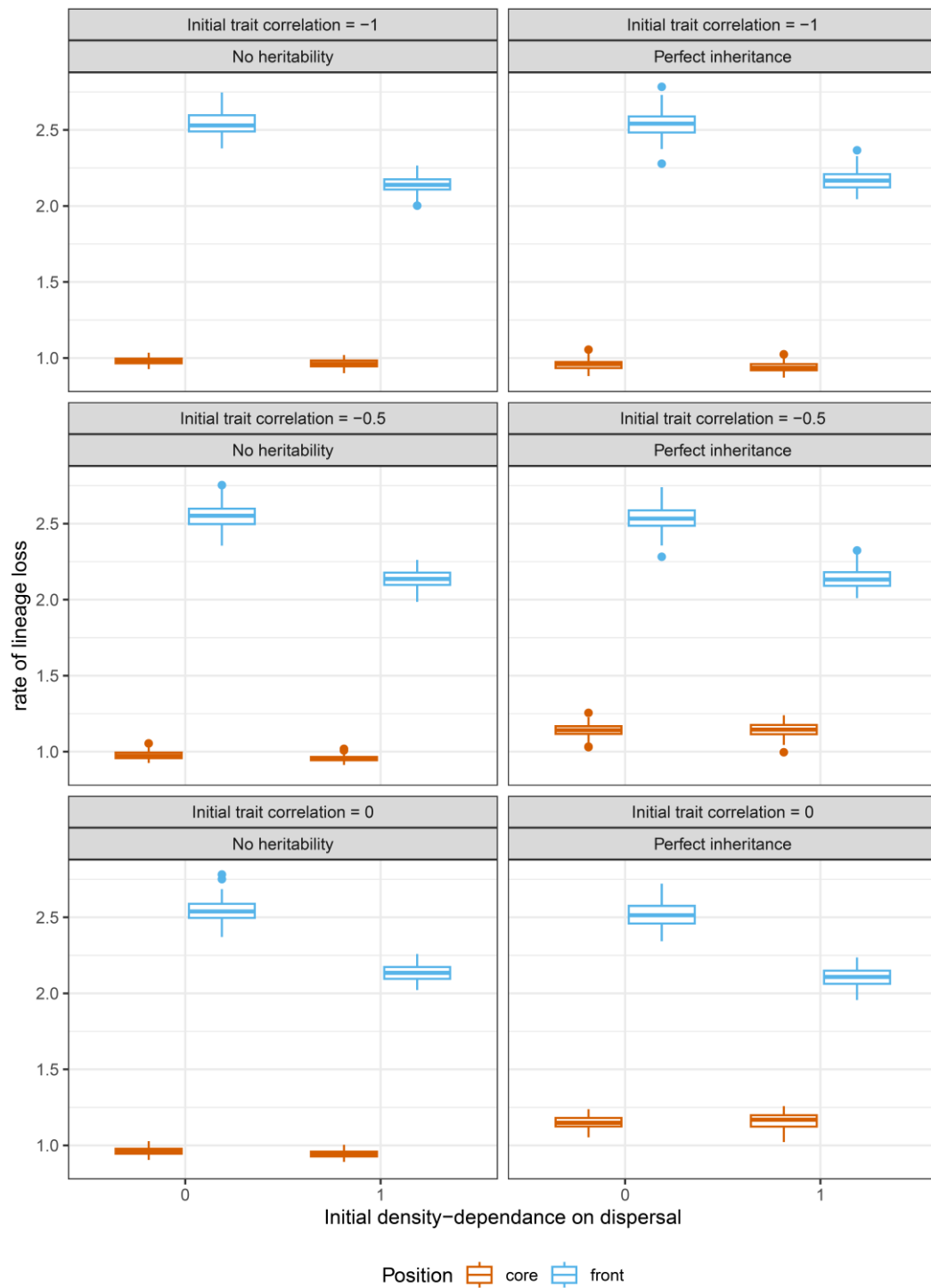
### Supplementary Material 1: Detailed plots of traits evolution

The following plots represent the mean values per patch of four heritable traits within our simulated populations, among the different treatments and/or positions within the expansion. [Supplementary Figure III.5](#) and [Supplementary Figure III.6](#) allows us to verify if simulations behaved according to the literature, one of many checks done to ensure that our model was correct. Indeed, we expected from competition-colonization theory to have a spatial sorting between good competitors (high juvenile survival at high density) in the core and good colonizers (high fecundity at low density) in the front (Levins & Culver, 1971; Yu & Wilson, 2001). [Supplementary Figure III.1](#), [SIII.2](#), [SIII.3](#) and [SIII.4](#), are a raw representation of [Figure III.2](#), [III.3](#), [III.4](#) and [III.5](#), presented in the main paper.

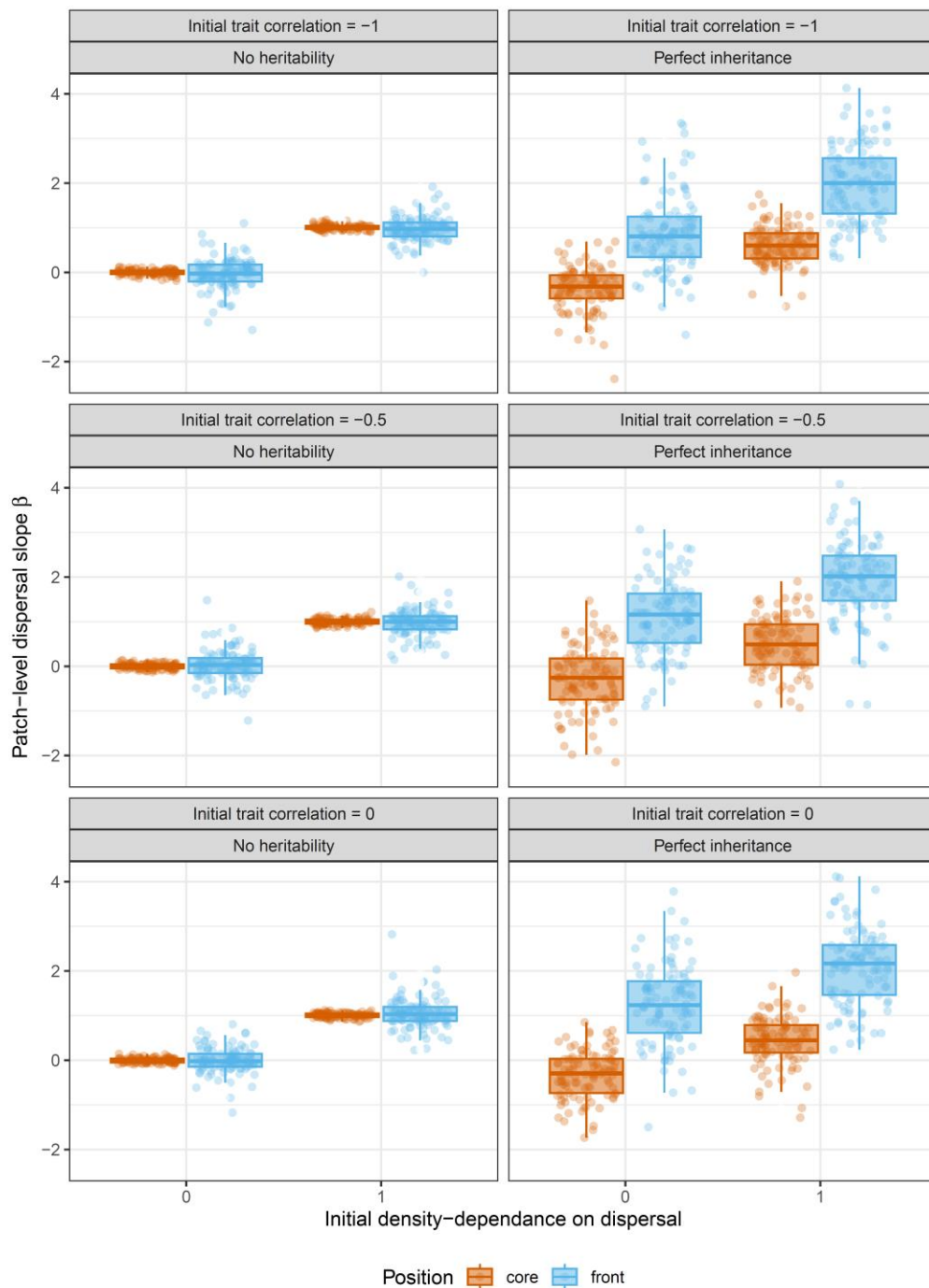


**Supplementary Figure III.1: Plot of neutral alleles retention in function of the different treatments.**

Coloured points represent each singular observation while boxplots represent the median, 25th and 75th percentiles.

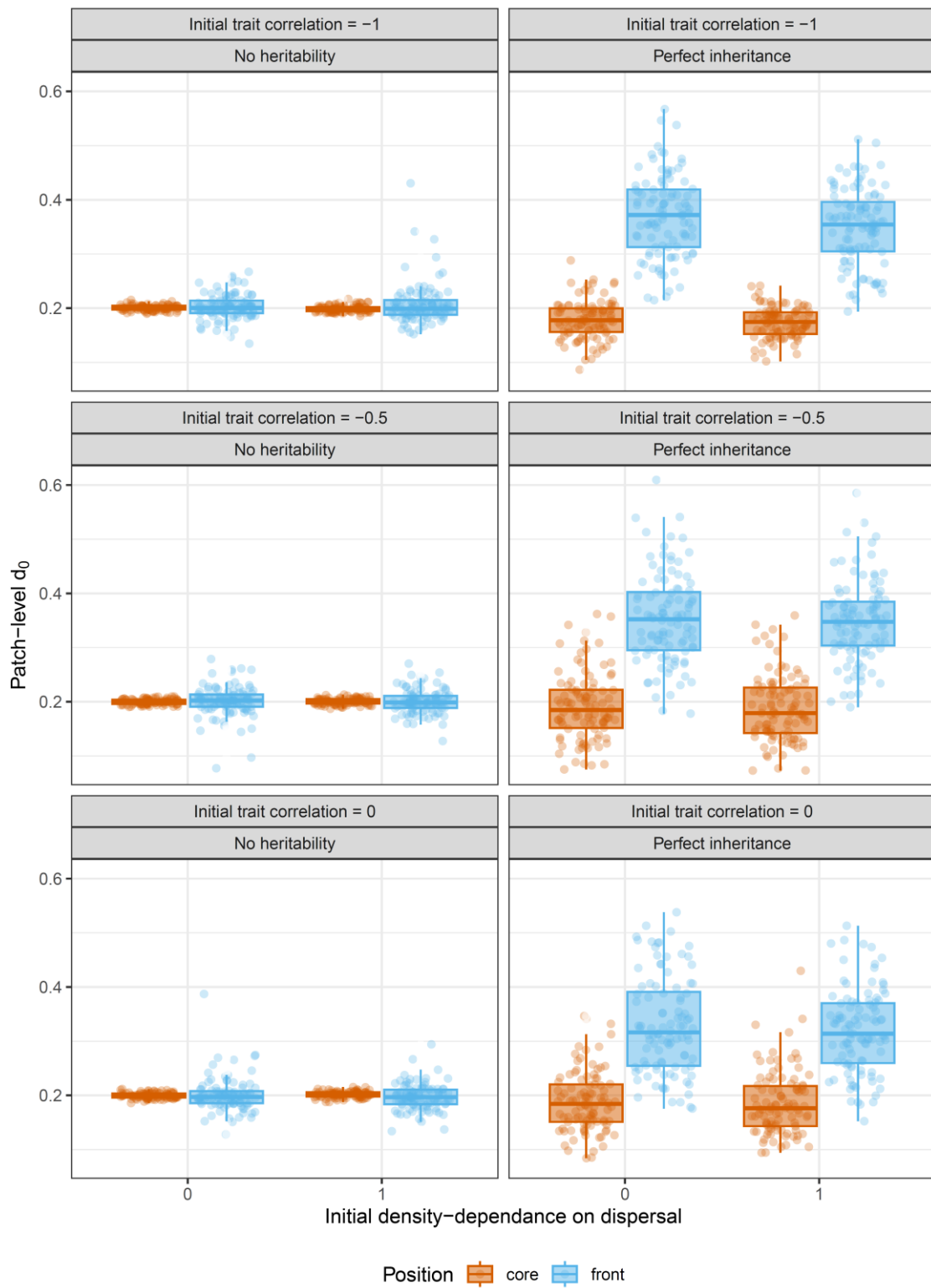


**Supplementary Figure III.2: Lineage decay rates in range core and front.**  
 Boxplots represent the median, 25th and 75th percentiles.



**Supplementary Figure III.3: Mean dispersal slope distribution as a function of different treatments.**

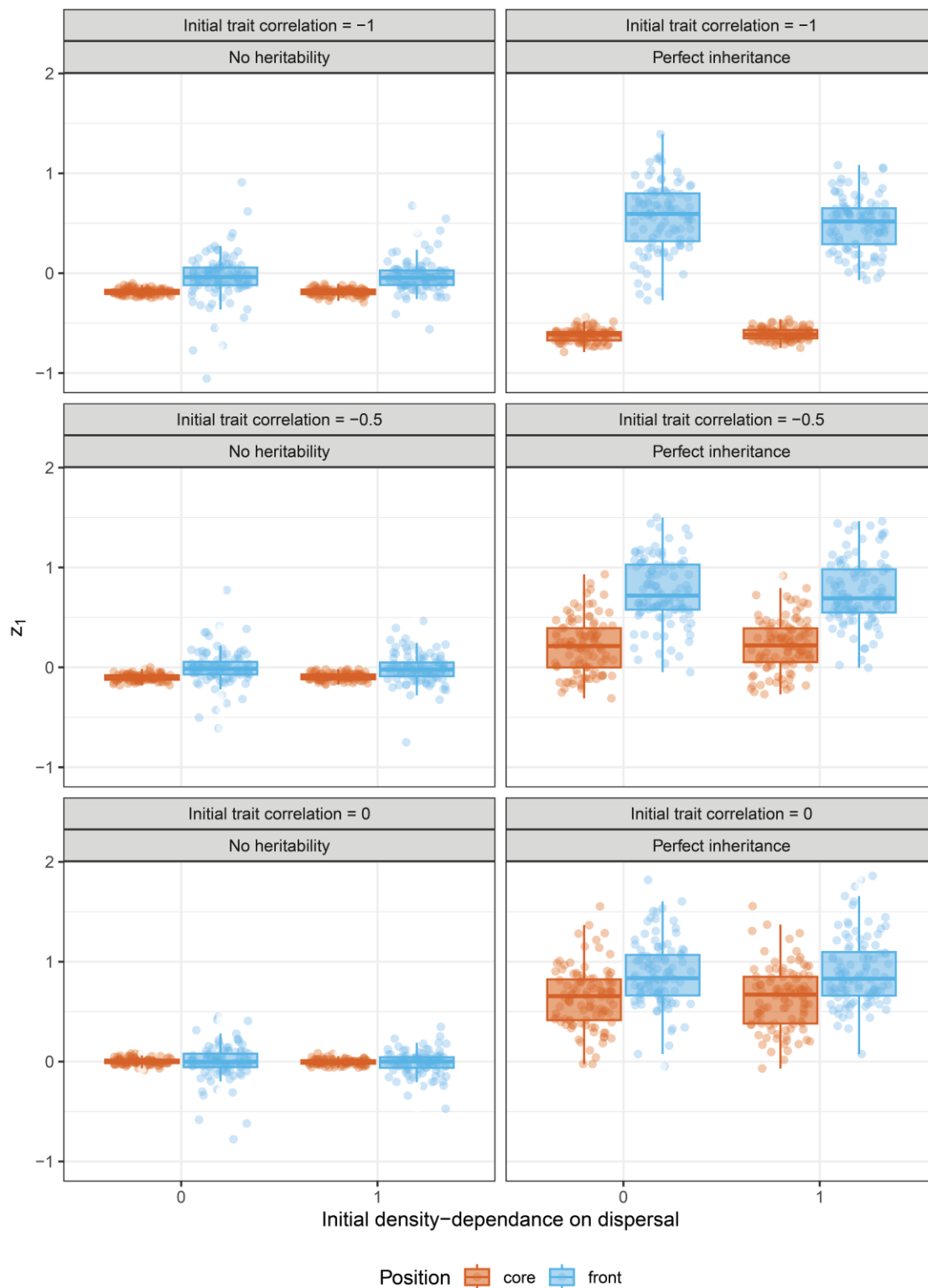
Boxplots represent the median, 25th and 75th percentiles. The mean observed values of all individuals for every replicate within core or front patches are also shown by coloured points.



**Supplementary Figure III.4: Patch means logit dispersal probability at density 0 depending on the different treatments.**

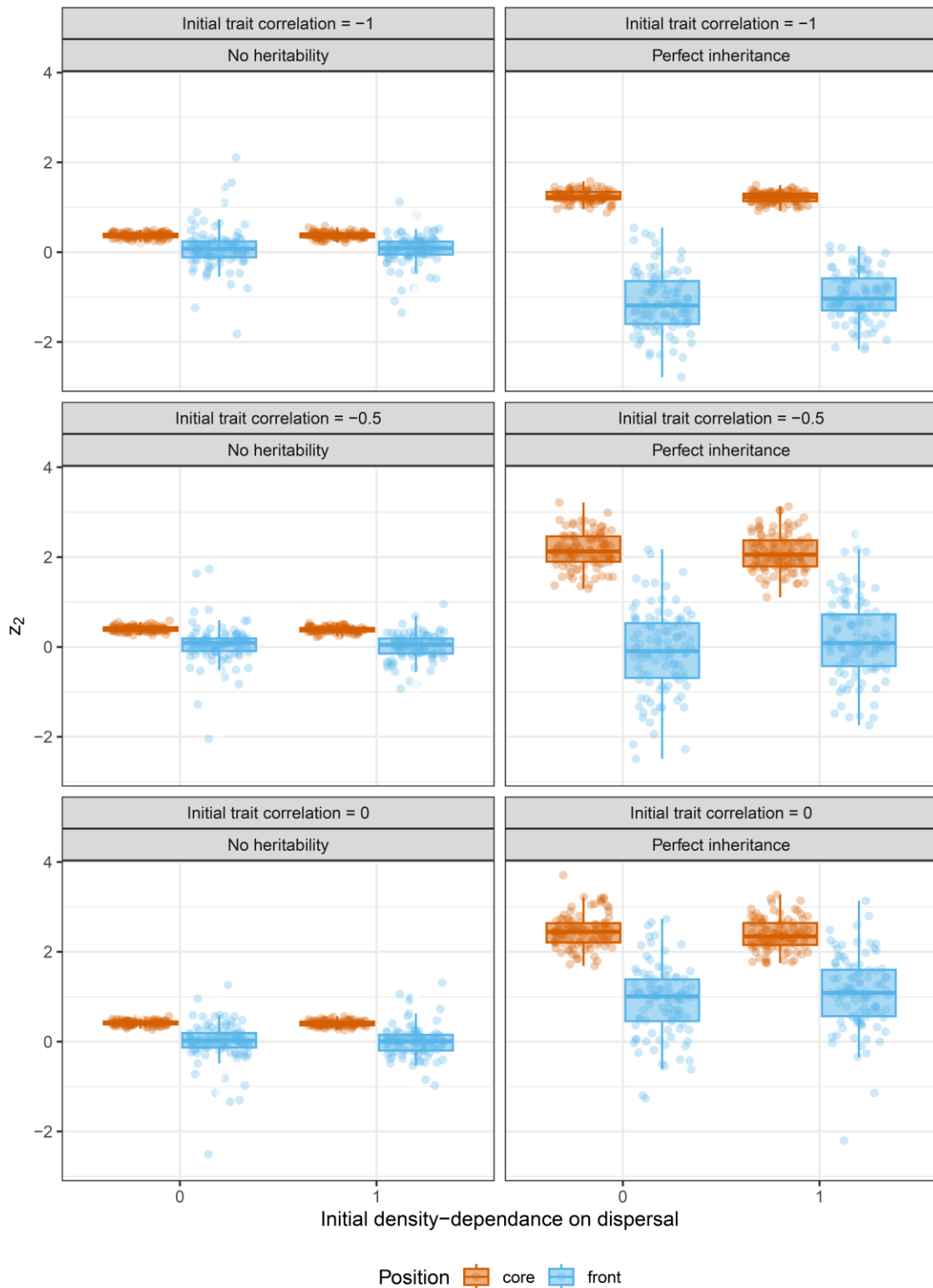
Boxplots represent the median, 25th and 75th percentiles. Mean core/front patch observed values for every replicate are also shown by coloured points.





**Supplementary Figure III.5: Mean individual variation in adult fecundity as a function of different treatments.**

While boxplots represent the median, 25th and 75th percentiles. The mean observed values of all individuals for every replicate within core or front patches are also shown by coloured points.



**Supplementary Figure III.6: Mean individual variation in juvenile survival as a function of different treatments.**

While boxplots represent the median, 25th and 75th percentiles. The mean observed values of all individuals for every replicate within core or front patches are also shown by coloured points.

## Supplementary references

Levins R, Culver D (1971) Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences*, 68, 1246–1248.

<https://doi.org/10.1073/pnas.68.6.1246>

Yu DW, Wilson HB (2001) The competition-colonization trade-off is dead; long live the competition-colonization trade-off. *The American Naturalist*, 158, 49–63.

<https://doi.org/10.1086/320865>

**To sum up :**

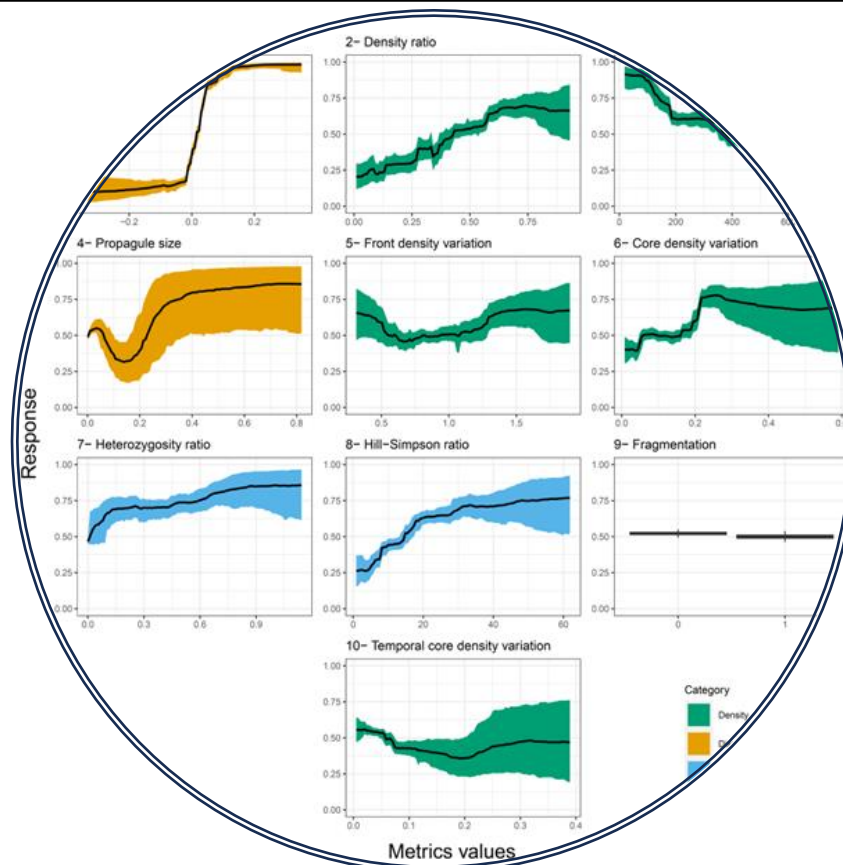
- Expected spatial sorting of competitors (in range core) and colonisers (in the leading edge) was observed.
- We also observed the expected positive influence of initial positive density-dependence in dispersal on neutral genetic diversity. However, a stronger effect was observed on the temporal neutral genetic diversity metric.
- We hypothesise that this difference results from variations in positive density-dependence in dispersal depending on the spatial location of patches in an expansions
- Based on the value of positive density-dependence, evolution tends to make expansions more pushed
- Trait correlation does not have a significant effect neither positive density-dependent dispersal's evolution nor neutral genetic diversity



## IV- Finding a metric set to estimate the pushed/pulled continuum position of a biological expansion

### Article 4: How to discriminate between pulled and pushed expansion waves: finding operational indicators for biological expansions

*Note that, as of now, this chapter is centred on providing a preliminary proof-of-concept for the idea of predicting "pushedness" from a set of demographic and genetic metrics. As such, it focuses on pushed expansions created by density-dependent dispersal only. A future goal is to generalise our analysis to pushed expansions generated through various mechanisms, including Allee effects; this would give us important insights into whether or not mechanisms generating pushed expansions (positive density-dependence in dispersal or reproduction) lead to similar dynamics or if we might need to set separate demographic and genetic expectations (and therefore separate predictive models) based on the source of the density-dependence.*



## Bayesian Additive Regression Trees (BART)

In this chapter, we try to predict drivers or proxies of pushedness (the presence of positive density-dependence in dispersal or the value of one genetic diversity measure) based on a compilation of metrics values extracted from the simulated expanding populations. The attempt to predict the presence/absence of density-dependence represents a classification problem, for which many methods have been developed. A few examples include Linear Discriminant Analysis (LDA) (Balakrishnama & Ganapathiraju, 1998), frequently used in metabolomics (Worley & Powers, 2012), or logistic regression models and extensions (among them the Bayesian Ordinal Logistic Regression/ Models or OLR, for more than two ordered categories (Bürkner & Vuorre, 2019)). The choice of the method depends on the aims of the study and the dataset, each method having its advantages and disadvantages (linearity constraints, binary classification only, accounting or not for uncertainty...).

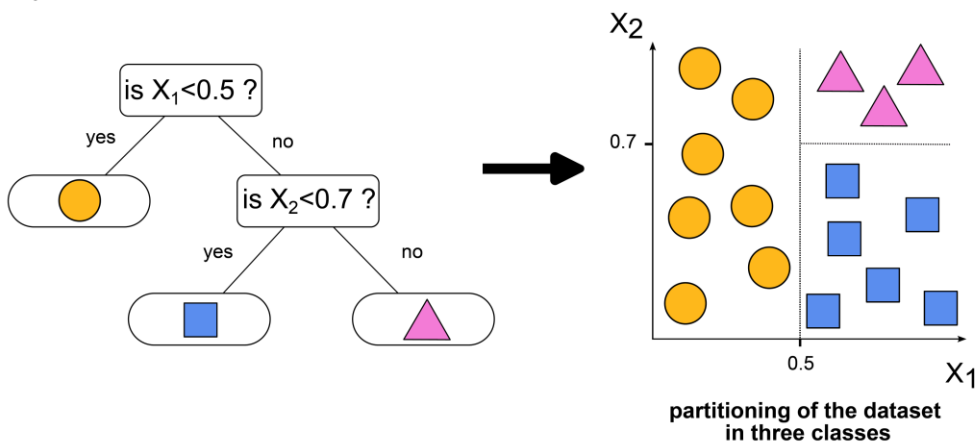
However, as we are here attempting to predict both continuous (genetic diversity) and binary responses, there is an appeal in methods that are able to do both regression and classification, such as random forests (RF) (Breiman, 2001) and other decision-tree based methods. We employed the Bayesian Additive Regression Tree (BART) method (Chipman et al., 2010), as it fits this prerequisite and also incurs lower risks of overfitting (i.e. the inability for the model to be generalised on unknown datasets because it is too closely fitted to the training data), compared to RF. BART, Random Forest, and other randomised tree methods can be seen as ensemble methods, in that they train many simple estimators or *learners* (here decision trees, [Figure IV.1](#)) and combine them to solve the same problem (Zhou, 2012; Martin et al., 2021). The downside of decision trees is that their flexibility can make it easy to generate complex trees, isolating each datapoint within its own partition, resulting in overfitting. For that, BART draw from Bayesian inference by imposing priors favouring many trees with low depth and fit (e.g. *weak learners*) where each tree could not explain the entire dataset but only a tiny portion (Chipman et al., 2010). Combining the prior distribution of decision tree's form with the data present will generate a posterior distribution of one model's prediction. Sampling from a posterior distribution allows for easily quantifiable uncertainty of our predictions (but not only, see our

paragraph about partial-dependence plots below) compared to other sum-of-tree methods without a Bayesian implementation.

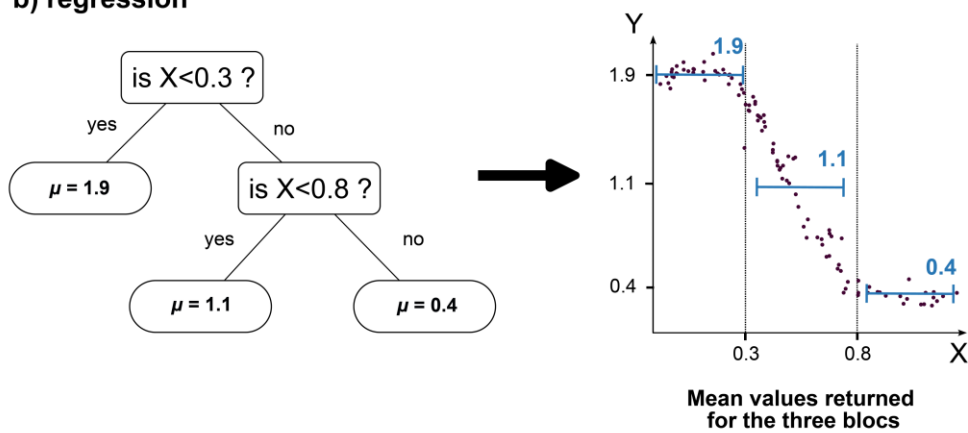
The study presented in this chapter represents a first attempt to use a set of metrics to predict indicators of pushedness, and for that, we used a wide variety of metrics to include in our set. BART is among the methods that allows us to look at the most important metrics to predict the response. To measure metric contribution to the predictive power here, we look at the number of times a metric is used within a splitting rule among all the decision trees (using the *varimp* function presented in Carlson, 2020). Knowing a variable importance rank could help us discard the metrics with little to no predicting power, letting us focus our priority during analyses and collection processes on the most valuable metrics. Furthermore, we can observe how the change of one metric can influence the response's value, when all other metrics are kept constant with partial-dependence plots (Friedman, 2001; Chipman et al., 2010). Such plots will allow us to compare the expected influence of one metric variation on the response, based on our knowledge of pushed/pulled expansions, to its actual effect. While partial dependence plots are not exclusive to BART, the Bayesian aspect of the method allows for easily quantifiable uncertainty, as proven in Carlson (2020) by comparing out-of-the-box implementations of partial dependence curves generated by a single-instance BART implementation and a single-instance boosted regression trees implementation.



## a) classification



## b) regression



**Figure IV.1: Representation of a binary decision tree and the resulting partitioning.**

Each internal node represents a splitting rule leading to another splitting rule or a terminal node. The terminal nodes are A) the class label (circle, triangle or square) in case of classification or B) a mean value of each block partitioning the data for regressions. Note that regressions can also return other descriptions of the blocks, such as the median or a linear regression. Adapted from Martin et al. (2021).

# Article 4: How to discriminate between pulled and pushed expansion waves: finding operational indicators for biological expansions

Chloé Guicharnaud, Pablo Le-Guern-Fiallo, Maxime Dahirel, Elodie Vercken

## Introduction

Knowing how a species' range expands or shifts in a habitat is essential in the context of biological invasions. It is even more so nowadays when climate change can also increase the possibility of species shifting their range to more or newly suitable habitats. Those modifications can lead to significant environmental impacts and have ecological and economic consequences (Pimentel et al., 2005; Diagne et al., 2020, 2021). For example, one of the many invasive species in East America, the Emerald ash borer (*Agrilus planipennis*), was first sighted in the U.S. in 2002 and is now present in most Eastern U.S. states and the Canadian provinces of Ontario and Quebec. Native to Asia, they infect and kill ash trees, and it was estimated that the response to the infestation would cost up to \$10.7 billion for the years 2009 to 2019 (Kovacs et al., 2010). One part of invasion biology (respectively climate change biology) is trying to determine how invasive species (respectively climate-tracking species) spread and extrapolate their future dynamics thanks to modelling.

A detailed understanding of all the major characteristics of an expansion can be needed to respond correctly to, help, or control spread. In the case of e.g., range-shifting species tracking climate change, management plans using genetic diversity as a criterion for choosing one management strategy or another can fail if diversity is not correctly estimated. Conservation strategies can also wrongly choose conservation sites when based on classical genetic diversity indices, as presented in Paz-Vinas et al. (2018). In the case of the invasive spongy moth *Lymantria dispar*, the whole management strategy as implemented in the STS (Slow the Spread) program is based on the knowledge of the

presence of a strong Allee effect (Tobin et al., 2009; Walter et al., 2020), meaning that below a specific density, the per-capita population growth rate becomes negative (instead of just lowering in the case of a weak Allee effect) (Berec et al., 2007). The wrong estimation of some ecological parameters can also lead to the initially intentional introduction of a species for classical biological control getting out of hand, as was the case for the Harlequin Ladybug (*Harmonia axyridis*). First introduced as a biocontrol agent against aphids or coccids, it is now an invasive species endangering native species of ladybugs, as their wide host range and tendency to prey on other ladybug larvae when the usual preys are few have been wrongly estimated (Camacho-Cervantes et al., 2017). This is why managing a species' propagation relies heavily on accurately understanding its ecological dynamics. Because ecological and evolutionary dynamics and their interactions can vary a lot between species (Renault et al., 2018; De Meester et al., 2019), many heterogeneous patterns of invasions exist, making it more challenging to develop a predictive invasion biology framework.

Researchers attempting to study or predict the propagation of a species across a new environment or a change in the pre-established range caused by external perturbations often rely on the mathematical concept of travelling waves. This concept has been applied in many fields other than in ecology, wherever the presence of an invasion front is possible, be it in physics (crystal growth), chemistry (chemical reaction and diffusion), or even medical science (propagation of cancer cells) (van Saarloos, 2003; Joshi et al., 2018). In mathematics, travelling waves represent particular solutions of reaction-diffusion models where the velocity and the wavefront profile are constant. Reaction-diffusion models represent the spread of a quantity  $u(t, x)$  in time and space, which is typically in ecology a density of organisms and/or alleles. The most common models in this category build on the Fisher-KPP model (Kolmogorov et al., 1937; Fisher, 1937). Those travelling waves can be classified into two categories: pulled and pushed waves. Pulled waves happen when spread (which results from a combination of growth and dispersal) is maximal at low densities (i.e., in the recently founded populations at the edge of the wave). Hence, the expansion is "pulled" ahead by its most advanced populations. However, the maximum growth and dispersal rates do not always occur at low densities. When growth and/or dispersal are maximal at intermediate or high densities, this leads

to pushed waves, where the wave and its velocity are driven by the dynamics of a region farther behind the expansion's edge (Stokes, 1976; Birzu et al., 2019; Lewis, 2019).

Pushed waves are favoured by ecological mechanisms known to generate or amplify positive density-dependence in spread. This includes Allee effects (Gandhi et al., 2016), positive density-dependent dispersal (Birzu et al., 2019), or the presence of a competitor (Bonneton et al., 2014). These mechanisms have well-studied ecological and evolutionary consequences, and accordingly, previous results proved that some demographic, genetic, and evolutionary properties can vary depending on the type of the expansion (Roques et al., 2012; Bonneton et al., 2014; Gandhi et al., 2016; Birzu et al., 2021).

One main oversight of the literature is that most of the time, only the Allee effect is mentioned as a mechanism generating pushed expansions (with some authors even suggesting that Allee effects are necessary to generate pushed expansions, e.g. Foutel-Rodier & Etheridge, 2020), while the possibility of pushed waves caused by density-dependent dispersal is overlooked. It is only in the last decade that a few articles taking density-dependent dispersal into account have emerged (Sullivan et al., 2017; Kawasaki et al., 2017; Wang et al., 2019; Birzu et al., 2019; Haond et al., 2021). This is surprising because, given the high frequency of positive density-dependent dispersal in nature (Harman et al., 2020), dispersal-caused pushed waves may be particularly common, possibly more than Allee-mediated ones. Another nuance to add is that according to several authors (Birzu et al., 2018; Gandhi et al., 2019), the dichotomy between pulled and pushed is less strict than first thought in theory. It might be more appropriate to think of range expansions as spanning a continuum of more or less pushed waves, including an intermediate group neither pulled nor pushed according to usual criteria, called 'semi-pushed' waves (Birzu et al., 2018).

Knowing where sit an expanding population/species on the pushed/pulled gradient is useful as spread velocity (Zhu et al., 2023) or neutral genetic diversity (Garnier et al., 2012; Birzu et al., 2019) will vary and models based on pulled assumptions will not give good predictions on a pushed expansion. A classical way to determine the pushedness of an expansion relies on comparing observed expansion speed to predicted speed based on population growth and dispersal at low density (Lewis & Kareiva, 1993; Kot et al., 1996;

Roques et al., 2012; Birzu et al., 2018; Gandhi et al., 2019). However, while this may be doable in theoretical or experimental studies, acquiring these low-density trait data can be technically challenging, time-consuming, and sometimes simply impossible, especially in species that cannot be reared or observed easily, which includes many invasive or threatened species. On the other hand, some studies hint that other metrics differ between pushed and pulled waves and could be used as indirect indicators. These include the dynamics of genetic diversity (Roques et al., 2012; Birzu et al., 2018) or the relation between speed and carrying capacity (Haond et al., 2021). Given that the underlying causal mechanism shaping pushed/pulled dynamics is density-dependence in growth and/or dispersal, and that such density-dependence is known to have widespread demographic impacts (Stevens & Bonsall, 2011; Row et al., 2014; Cronin et al., 2020), we believe that other additional indicators could conceivably be used.

Our goal in this context is to test a set of indicators that could be easily measured in surveys of biological expansions to see if they can help distinguish between the types of expansion, with the long-term objective of being able to predict and estimate the proportion of pushed expansions in nature. We believe it is possible to sidestep the inherent difficulty associated with measuring life-history traits at very low density (close to 0) *in natura* (as even finding low-density expansion edges can be challenging, e.g. Fitzpatrick et al., 2009) that prevents the generalised use of "classical" indicators of pushedness (e.g. the ratio between observed velocity and theoretically predicted "pulled" speed; Birzu et al., 2018; Gandhi et al., 2019), by using a set of indicators that may be less closely related to the underlying causal mechanism, but much easier to measure and with enough predictive power to classify biological expansions on the pushed/pulled gradient.

To find and test a panel of optimal indicators, we generated simulated populations using individual-based models, meaning that the fate of an agent in the model, here an individual in the population, depends on individual behavioural rules or one's neighbours and their actions (DeAngelis & Grimm, 2014). Playing with the ecological mechanisms generating these simulated populations gave us access to a continuum of more or less pushed and pulled waves. We then classified simulations into pulled and pushed waves based on the presence/absence of a positive-density dependence (the causal mechanism generating pushed expansions) or ranked them on a gradient based on neutral genetic

diversity (expected to be more conserved in pushed expansions (expected to be more conserved in pushed expansions, Bonnefon et al., 2014)). We then used Bayesian Additive Regression Trees (Chipman et al., 2010) to predict the above metrics of "pushedness" from a set of summary demographic and genetic summary statistics extracted from the simulations, which represent measurements thought to be "easier" to observe in realistic/natural settings. We also ranked these predictors to determine the most important for correctly predicting the response.

## Materials and Methods

### *The Individual-Based Model*

We wrote an individual-based model simulating range expansions using the NetLogo programming language (Wilensky, 1999), version 6.2.0. Following most theoretical works on pushed waves, we studied propagation in 1-dimensional discrete landscapes (like Birzu et al., 2019). Individuals are haploid, reproduce clonally, and possess a neutral locus *Loc* that can take either the allelic values 1 or 0. Generations are non-overlapping. Simulations start by releasing an initial population size of  $K$  adults, where  $K$  is one patch's equilibrium population size, in the leftmost patch of the landscape (i.e. patch with  $x = 0$ ). Those starting individuals are randomly assigned one of the two neutral alleles alongside a unique lineage identifier *lineageID*. The following life cycle occurs for each generation until the end of the run: the adults disperse following a dispersal function before reproducing clonally, transmitting their neutral allele to their offspring, and then die right after. The offspring of these individuals then become an adult if they survive the juvenile stage and start a new life cycle. Within a given expansion, the only individual parameters that vary between individuals (and are inherited from the parent) are the *Loc* allelic value and the lineage identifier *lineageID*. Adding density-dependence in dispersal (positive or negative) is possible alongside dispersal mortality.

Dispersal is Bernoulli-distributed, with the dispersal probability being  $D = \text{logit}^{-1} \left( \text{logit}(d_0) + \beta \times \frac{N}{K} \right)$ . Dispersal, therefore, depends on only two ecologically meaningful parameters: the hypothetical dispersal probability at density 0  $d_0$  and the slope  $\beta$  of the relationship between relative density and dispersal rate. Dispersers

move to one of the adjacent patches. If an individual disperses, there is a probability  $m$  for it to die instead of settling on another patch, mimicking dispersal costs.

After the dispersal phase, the number of offspring per individual is drawn from  $\text{Poisson}(\lambda)$ , with  $\lambda = e^{r_0 \left(1 - \left(\frac{N}{K}\right)\right)}$ , where  $r_0$  is the average low-density growth rate. Juvenile survival is Bernoulli-distributed, with individual juvenile survival probability being also density-dependent, such as  $S = e^{\left(-\log\left(\frac{1}{s_k}\right) \times \left(\frac{N}{K}\right)\right)}$ , where  $s_k$  is the individual expected survival rate when  $N = K$ .

#### *Population simulations*

The *nlrX* package (Salecker et al., 2019) and R version 4.3.0 (R Core Team, 2023) were used to run our NetLogo simulations. Simulations ran for a maximum of 50 generations per run or until all populations went extinct (in practice, no replicate went entirely extinct). A variety of parameter combinations were used to generate a wide range of expansions for a total of 972 unique sets of initial conditions (hereafter "scenarios") (Table IV-1). With ten replicates per scenario, we ended with 9720 generated simulated expansions. In practice, only 9369 simulations were analysed as one metric of interest (the propagule size, see Table IV-2) could not be retrieved for 351 expansions (see Discussion). This is because these expansions did not create new edge patches during the last five generations, which is when our predictors are collected (see below).

**Table IV-1: Simulation parameter values chosen in our different simulation sets.**

All scenarios are examined.

	<i>Description</i>	<i>Values</i>	<i>Commentary</i>
<b>SIMULATION PARAMETERS</b>			
<b>USED TO GENERATE DATA WITH/WITHOUT POSITIVE DENSITY-DEPENDENT DISPERSAL</b>			
$\beta$	Average strength of density-dependent dispersal	-0.5 ; 0 ; 0.5 ; 1	Used to create the binary response DDD+
<b>NOISE AND/OR TRAIT DIVERSITY</b>			
<b>ONLY USED FOR NOISE AND/OR TRAIT DIVERSITY</b>			
$\text{logit}(d_0)$	Average dispersal rates at density 0 on a logit scale	0.1 ; 0.25 ; 0.5	
$s_K$	Average juvenile survival at density K	0.8 ; 0.9 ; 0.99	
$K$	Patches carrying capacity and the maximum number of unique lineages	250 ; 500 ; 750	
<b>ALSO USED TO CREATE SUB-DATASET TO EVALUATE MODEL PERFORMANCE</b>			
$r_0$	Average low-density growth rate	$\text{Log}(1.5)$ ; $\text{Log}(3)$ ; $\text{Log}(5)$	
$m$	Average dispersal mortality	0 ; 0.25 ; 0.5	It is also used for fragmentation estimates (see 'Metric and responses compilation' section)

## Analyses

### *Metric and responses compilation*

- In our analyses, we then attempted to predict two responses:
- The presence of positive density-dependent dispersal (DDD+), a binary response created from the value of the dispersal slope  $\beta$  (DDD+ = 1 for every simulation with  $\beta > 0$ , and DDD+ = 0 otherwise)
- The degree of allelic retention in space (hereafter "allelic retention", is a continuous response ([Table IV-2](#) top). To estimate allelic retention, we divide an



expansion into two fractions depending on their *Loc* allele. Allelic retention is the ratio between the farthest position of the *Loc* allele lagging behind the expansion's edge and said edge position. In the extreme case of a pushed wave where no diversity is lost at the edge, all the components of the wave (here the alleles) should propagate at the same speed as the wave (so the ratio should be 1) (Bonneton et al., 2013). All else equal, the more an expansion is pulled, the more we should expect some alleles to lag behind the edge, reducing the mean allelic velocity. This variable was chosen as a response as it was previously shown that this neutral genetic diversity measure can be linked to density dependence in dispersal ([Appendix 1](#)) and is used here as an indirect measure.

The metrics we chose to use to predict the above responses can be classified into three categories, depending on the type of data collected: genetic metrics, population density-related metrics and dispersal-related metrics. All metrics are summarised in [Table IV-2](#).

The use of genetic metrics is justified because a key result of pushed expansion theory is that pulled waves are expected to lose genetic diversity at the edge faster than pushed waves (Bonneton et al., 2013; Birzu et al., 2019; Gandhi et al., 2019), as a consequence of a succession of founding effects. We calculated two metrics: first, the ratio between expected heterozygosity in the furthest patch and in the core (Bonneton et al., 2014) using the lineage identifier, then the Hill-Simpson index ratio  $HS = \frac{1}{1-He}$  (Roswell et al., 2021)

We selected metrics based on population density data because, at its core, the differentiation between pushed and pulled waves is due to differences in density dependence, which should have detectable consequences on population density along the expansion wave and especially at the edge (as in Williams & Levine, 2018). We calculated five metrics: the ratio between the density in the most advanced edge patch and the core ( $x = 0$ ); the variation within the five patches the nearest to the leading edge, related to the fact population density should decline at the edge at different rates in pushed and pulled waves (Williams et al., 2019). A similar measurement applied on the five at the expansion range core (closest to position  $x = 0$ ) was also calculated. The last two metrics are also related to core density, as core populations are easier to find and sample in nature than the exact range edge population, in alignment with this paper's goal

of using easy-to-get metrics. We selected the mean core density among the same five patches and a measure of the temporal density variation in the core patch during the last five generations.

Finally, three metrics are linked to dispersal or calculated from the dispersal costs parameter. We term the first one "habitat fragmentation" for simplicity: it is an arbitrary dichotomisation of the simulations' dispersal mortality parameter values (mortality of 0 represents low fragmentation, mortality > 0 high fragmentation), which can be interpreted as abstracting the level of habitat fragmentation ([Appendix 1](#)). This reflects (i) how in natural populations, individual surveyors may be able to at least roughly agree on which landscapes are high vs less fragmented, even if they don't agree on the exact fragmentation metric, and (ii) that estimates of habitat fragmentation should be easier to acquire than the precise dispersal costs, which are known to influence expansion dynamics and pushedness (Cote et al., 2017; Dahirel, Bertin, Haond, et al., 2021; Urquhart & Williams, 2021 see also [Appendix 1](#)). The second dispersal-related metric is the number of individuals at the start of a newly colonised edge population, or propagule size, with the expectation that new patches are founded by more individuals in pushed expansions (Williams & Levine, 2018). The final dispersal-related metric is the difference between observed dispersal rates in the core compared to the edge, as density-dependent dispersal should lead to higher dispersal in the core (where density is higher) than in the edge (Ochocki & Miller, 2017). We note that this last metric has a special status for two reasons. First, direct measurements of dispersal rates may be particularly complicated/time-costly to do in natural expansions, at least compared to our other chosen metrics. Second, unless patch population densities are highly variable, we expect this particular metric to be nothing more than a noisy measurement of the density dependence in dispersal (and therefore  $\beta/DDD+$ ). Therefore we may expect it to be one of the metrics having the most importance (at least for models with  $DDD+$  as a response, see below). To see if having this information on dispersal rates affects models' predictive power, we created a partial metric set without the dispersal rate difference and used it to fit our models.

*Estimating models' performance and metric importance*

All the model analyses are done with R version 4.3.0 (R Core Team, 2023) using the *embarcadero* package (Carlson, 2020), a wrapper around the *dbarts* package (Dorie, 2023), to fit Bayesian Additive Regression Trees (or BARTs) (Chipman et al., 2010).

We used BARTs to predict the presence/absence of positive density-dependent dispersal (DDD+) or the allelic retention value. Compared to other methods, BARTs have the advantage of being able to be applied for both classification (for DDD+) or regression (allelic retention) problems on top of offering considerable flexibility about parameters linearity or additivity (Hill et al., 2020) and lesser risks of overfitting compared to other methods. BART as a method is similar to Random Forest (RF) (Breiman, 2001) in that it uses randomly constructed trees, but each tree is adjusted to try to capture the signal still not accounted for in previous iterations like boosting methods

To account for the fact that not all sources of information are equally available in practice, and so not all metrics we proposed can be calculated, we fitted for each response (DDD+ and allelic retention) two models: once using the entirety of our metric set, then without the dispersal difference explanatory metric (the partial metric set including only the ones in bold in [Table IV-2](#)), for a total of four models (see [Figure IV.2](#)). We built for each metric partial dependence plots (showing the shape, strength and direction of its effect). We estimated its relative contribution to the model's predictive power on the training set. The latter allows us to order predictors by importance to see if one metric or metric category gives consistently more information and should be prioritised when collecting expansion data. Data were randomly split into training and testing sets before fitting models (using a three-quarter split, N = 7 026 and 2 343, respectively).

We evaluated model performance, i.e. how well it can predict the correct classification/value of the response, in different ways for classification (DDD+) and regression (allele retention) models ([Figure IV.2](#)). We used the True Skill Statistic (TSS) and the area under the Receiver-Operator Curve (AUC) as performance measures for the former. TSS is calculated as Sensitivity (true positive rate) + Specificity (true negative rate) - 1 and ranges between -1 and 1, with a score >0 indicating that a model predicts data better than random, with 1 being a perfect prediction (Allouche et al., 2006). AUC

measures the accuracy and uses the true positive rates but compares it with the false positive rate (Pepe et al., 2006). AUC values range from 0 to 1, with a score of 1 indicating perfect predictions. For regression models on allelic retention, we used the coefficient of determination  $R^2$  of the linear regression of observed on predicted values as a measure of predictive performance.

These performance metrics are by default "global" because they examine model quality over all scenarios. However, a given model may perform more successfully on some parts of the data than others, which may inform how it is used for further prediction. Therefore, for each model, we also calculated the aforementioned performance metrics on four sub-datasets, including only replicates with the highest/lowest  $r_0$  on one hand and the highest/lowest  $m$  on the other. We chose  $r_0$  or  $m$  as filters to partition the dataset because we showed in [Appendix 1](#) that they can qualitatively affect the "pushedness" of an expansion.

Table IV-2: All responses and metrics calculated from the generated simulations (or their parameters).

Metrics are separated into three categories related to which inside dynamic is observed: genetic diversity (in blue), population density (in green) or dispersal dynamics (in orange). Metrics in bold are the ones compiled in the partial set.

	DESCRIPTION	COMMENTARY/ EXPECTATION
<b>RESPONSES</b>		
<b>presence of positive density-dependent dispersal (DDD+)</b>	Separate expansions based on the presence or not of DDD+	If $\beta > 1$ , DDD+ = 1 else DDD+ = 0
<b>allelic retention</b>	Ratio between the position of the lagging allele and the edge patch	Expect values closer to 1 in pushed expansions
<b>METRICS</b>		
<b>GENETIC-BASED METRICS</b>		
<b>expected heterozygosity ratio</b>	Edge/core patches ratio of the expected heterozygosity $H_e$	Higher in pushed expansions
<b>Hill-Simpson index ratio</b>	Core/edge ratio of the calculated Hill-Simpson index	Higher in pushed expansions
<b>DENSITY-BASED METRICS</b>		
<b>front density variation</b>	Variation coefficient for the 5 patches present at the edge	Higher in pulled expansions
<b>core density variation</b>	Variation coefficient for the 5 patches present at the core	Higher in pulled expansions
<b>core mean density</b>	Mean population density of the 5 core patches	Higher in pushed expansions
<b>temporal core density variation</b>	Variation coefficient in the core patch between the 5 last generations	Higher in pulled expansions
<b>density ratio</b>	Ratio between edge and core patches	Higher in pushed expansions
<b>DISPERSAL-BASED METRICS</b>		
<b>propagule size</b>	Number of individuals in a new edge	Higher in pushed expansions
<b>fragmentation</b>	Proxy of habitat fragmentation based on dispersal mortality.	If $m = 0$ , fragmentation = 0 (and expected to be more pulled), otherwise 1.
<b>dispersal difference</b>	Difference between core and edge dispersal rates	Excluded from the partial metric set. Higher in pushed expansions

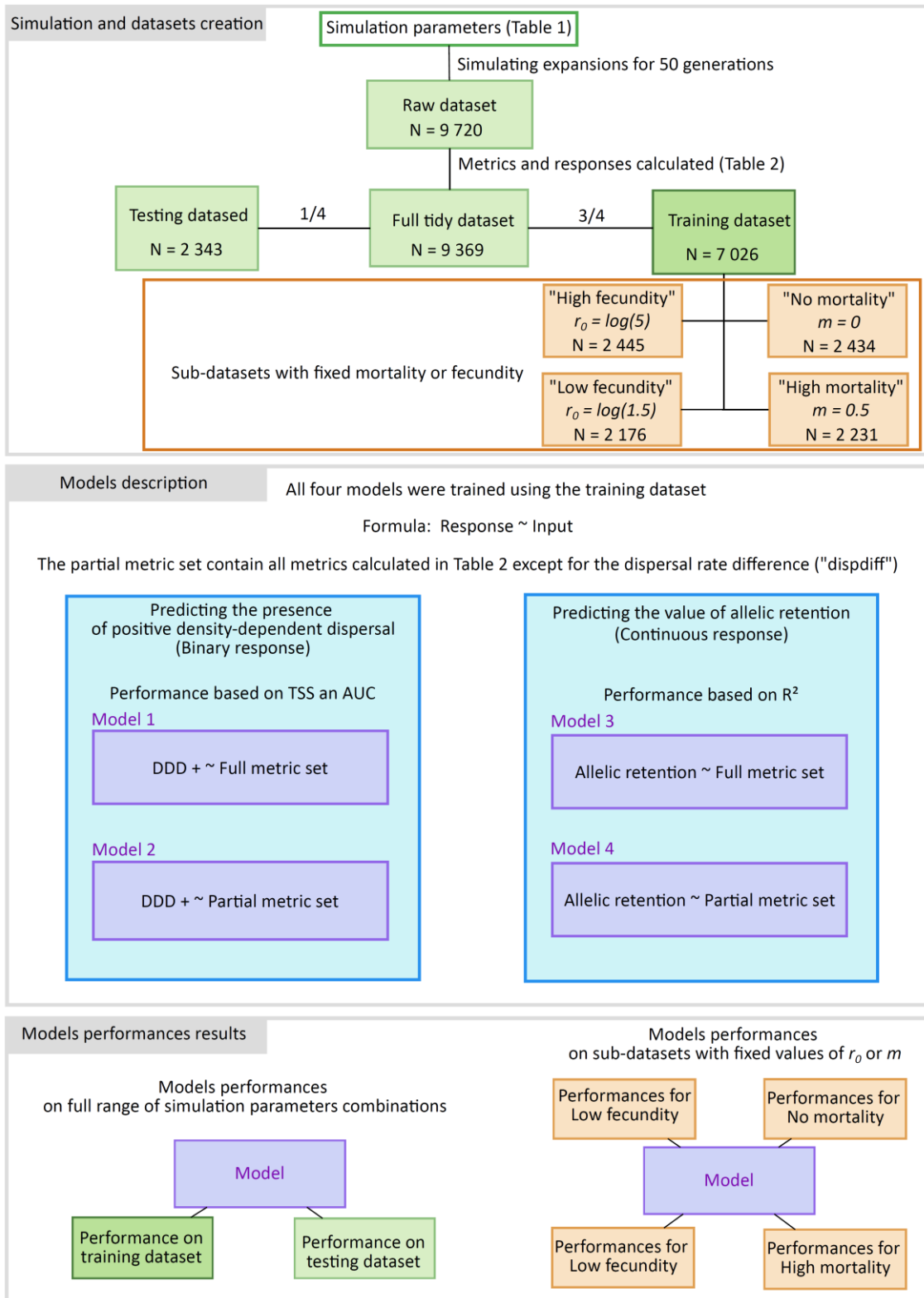


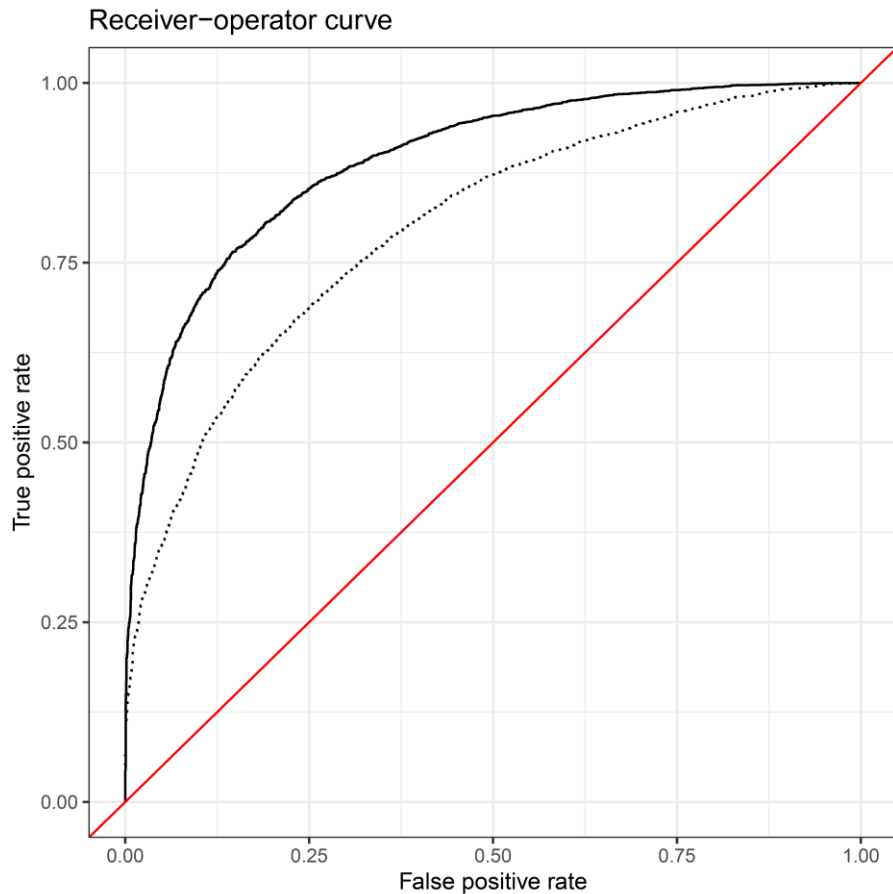
Figure IV.2: Schematic description of the different datasets and models explored.

TSS= True Skill Statistic. DDD+ = Positive density-dependent dispersal.

## Results

### *Models predictive power*

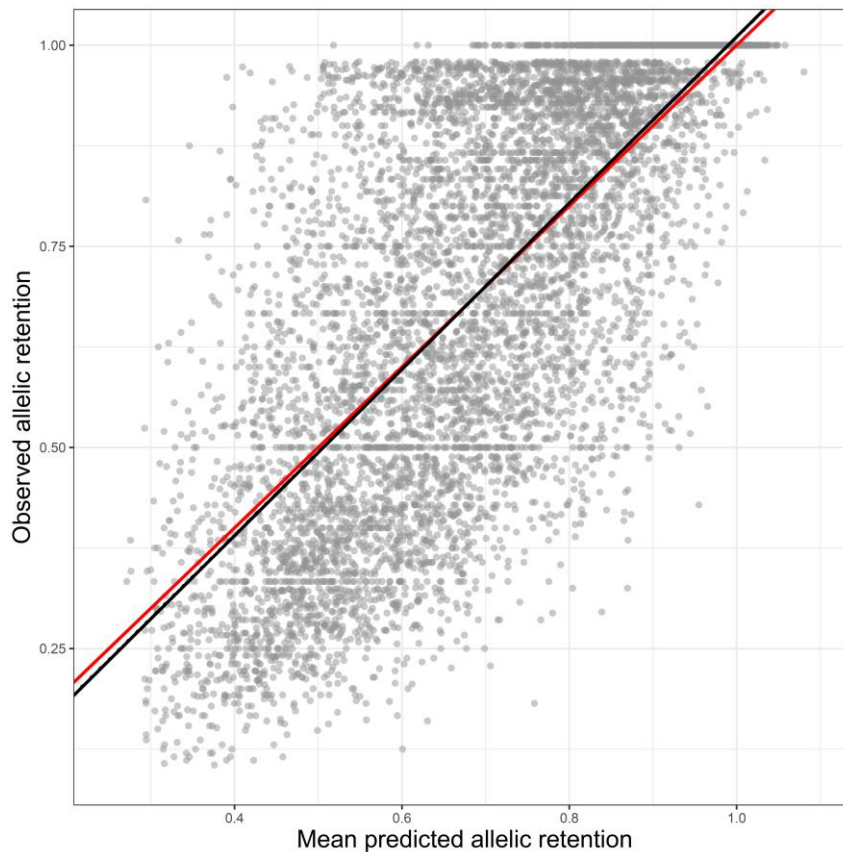
When analysing the performance of classification (DDD+) models, we observe a higher area under the curve (AUC) for the model fitted with the complete metric set (AUC = 0.89) than for the model fitted with the partial metric set (AUC = 0.80) (**Figure IV.3**). This is reflected in the TSS values in training and test sets (see **Table IV-3**). By contrast, regression models using the continuous allelic retention value as a response did not present significant variation in their performance between the full and partial metric set (**Table IV-3, Figure IV.4**). In each case, performance was worse on the testing dataset compared to the training set, indicating overfitting. While that decay was moderate in most cases, it was more marked for the TSS of the DDD+ model when fitted on a partial metric set (**Table IV-3**). When looking at model performance on sub-datasets, we see that all models performed better on the high fecundity subset than the low fecundity one and on the no dispersal mortality subset compared to the high mortality one (**Table IV-4**).



**Figure IV.3: Rate of true positives as a function of the false positive rate for models with positive density-dependence as a response.**

A high area between the curve and the red  $x = y$  line implies that the model can correctly predict the response value compared to random chance. The solid black curve corresponds to the model with the complete metric set inputted, and the dotted curve corresponds to the model with the partial metric set inputted.





**Figure IV.4: Observed allelic retention values in the training dataset as a function of the allelic retention values predicted by the model with allelic retention as a response.**

Both models with full or partial metric sets are so similar that the regression lines (full line for the model fitted on full metric set, dotted for the one fitted with partial metric set, but hidden behind the full line) nearly perfectly superimpose. The red line corresponds to  $x = y$ .

**Table IV-3: Models performances based on their True Skill Statistic (TSS) or R-squared ( $R^2$ ) values for training and testing datasets.**

For  $R^2$ , the 95% confidence interval is given in brackets.

		Train	Test
Models DDD+ (TSS)	All metrics	0.62	0.59
	Partial set	0.44	0.36
Models allelic retention ( $R^2$ )	All metrics	0.71 [0.70 ; 0.72]	0.66 [0.63; 0.68]
	Partial set	0.70 [0.68; 0.71]	0.64 [0.62; 0.66]

**Table IV-4: Models performances based on their True Skill Statistic (TSS) or R-squared (R<sup>2</sup>) values for each sub-dataset extracted from the training data.**

For R<sup>2</sup>, the 95% confidence interval is given in brackets.

		Sub-datasets			
		Low fecundity $r_0 = \log(1.5)$	High fecundity $r_0 = \log(5)$	No mortality $m = 0$	High mortality $m = 0.5$
Models DDD+ (TSS)	All metrics	0.54	0.67	0.65	0.59
	Partial set	0.34	0.50	0.46	0.43
Models allelic retention (R <sup>2</sup> )	All metrics	0.51 [0.48; 0.54]	0.70 [0.68; 0.72]	0.72 [0.70; 0.74]	0.68 [0.65; 0.70]
	Partial set	0.49 [0.46; 0.52]	0.70 [0.67; 0.72]	0.71 [0.69; 0.73]	0.67 [0.64; 0.69]

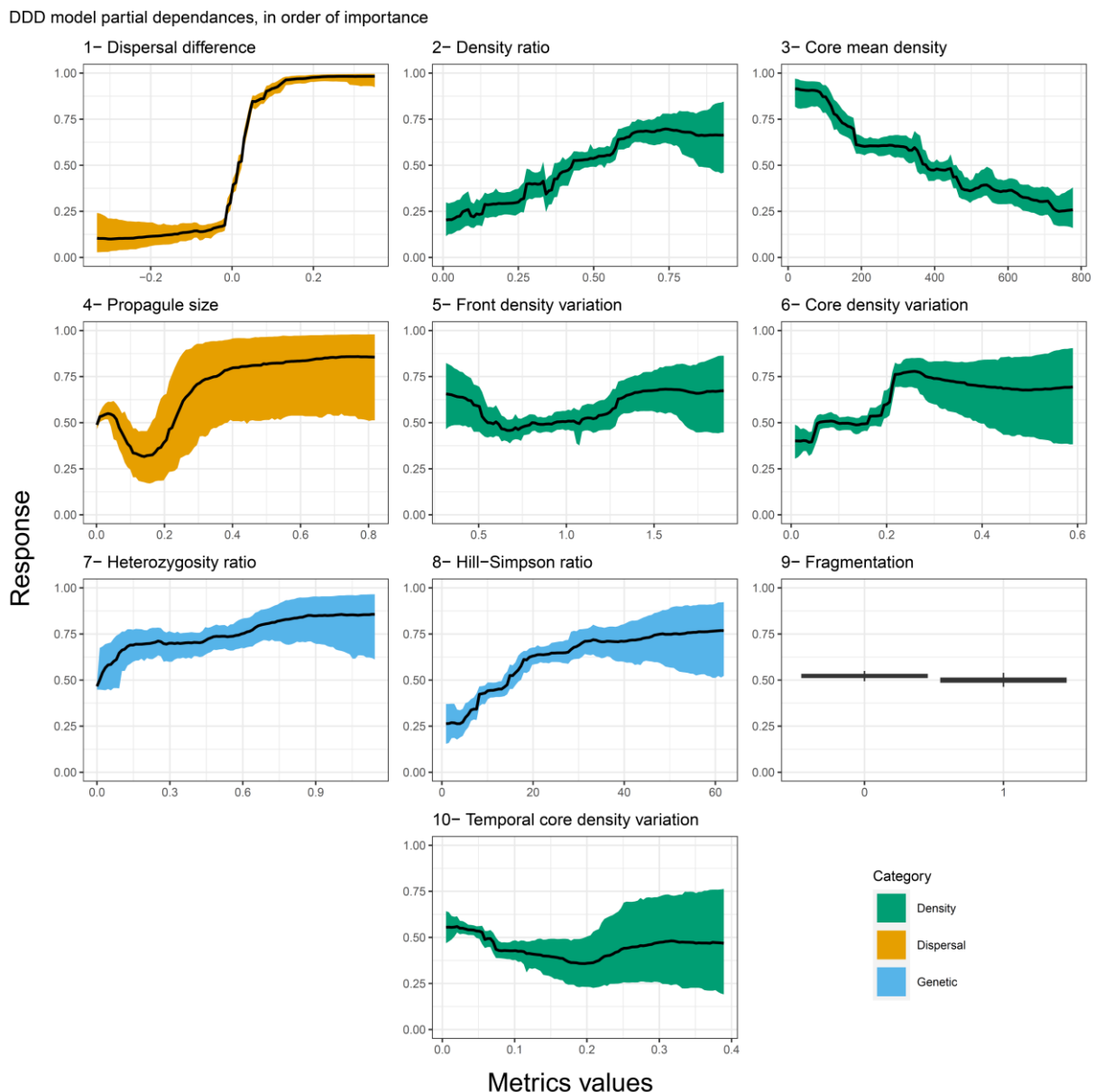
*Predictor metric importance*

As expected and almost by definition, the dispersal difference is the most important metric for predicting DDD+ when included ([Figure IV.5](#)). It is followed by two density metrics, the density ratio and mean core density and a second dispersal metric, the propagule size. Genetic metrics were only 7<sup>th</sup> and 8<sup>th</sup> in order of importance. When exploring partial dependence for the same model fitted on a partial metric set excluding dispersal difference, we see that the ranking of the other variables remains relatively stable (when accounting for uncertainty in ranking, see point estimates and intervals [Supplementary Figure IV.1](#)).

By contrast, for models with allelic retention as a response, the dispersal difference was not one of the most important metrics, but the density ratio, heterozygosity ratio, and edge density variation ([Figure IV.6](#)). Here again, when removing the dispersal difference from the predictor set, the ranking order of the remaining variable does not change meaningfully ([Supplementary Figure IV.1](#)). The least important metric for all models is the temporal core density variation [Figure IV.5](#), [Supplementary Figure IV.2](#)).

As the shape of partial dependence plots remains mostly unaltered by the conservation or removal of dispersal difference from the predictor set (compare [Figure IV.5](#) and [Figure IV.6](#) to [Supplementary Figure IV.2](#) and [Supplementary Figure IV.3](#)), we only present graphics for the former case in the main text. When it was possible to visually observe a variation of the response value depending on the metric value, we found that most of the

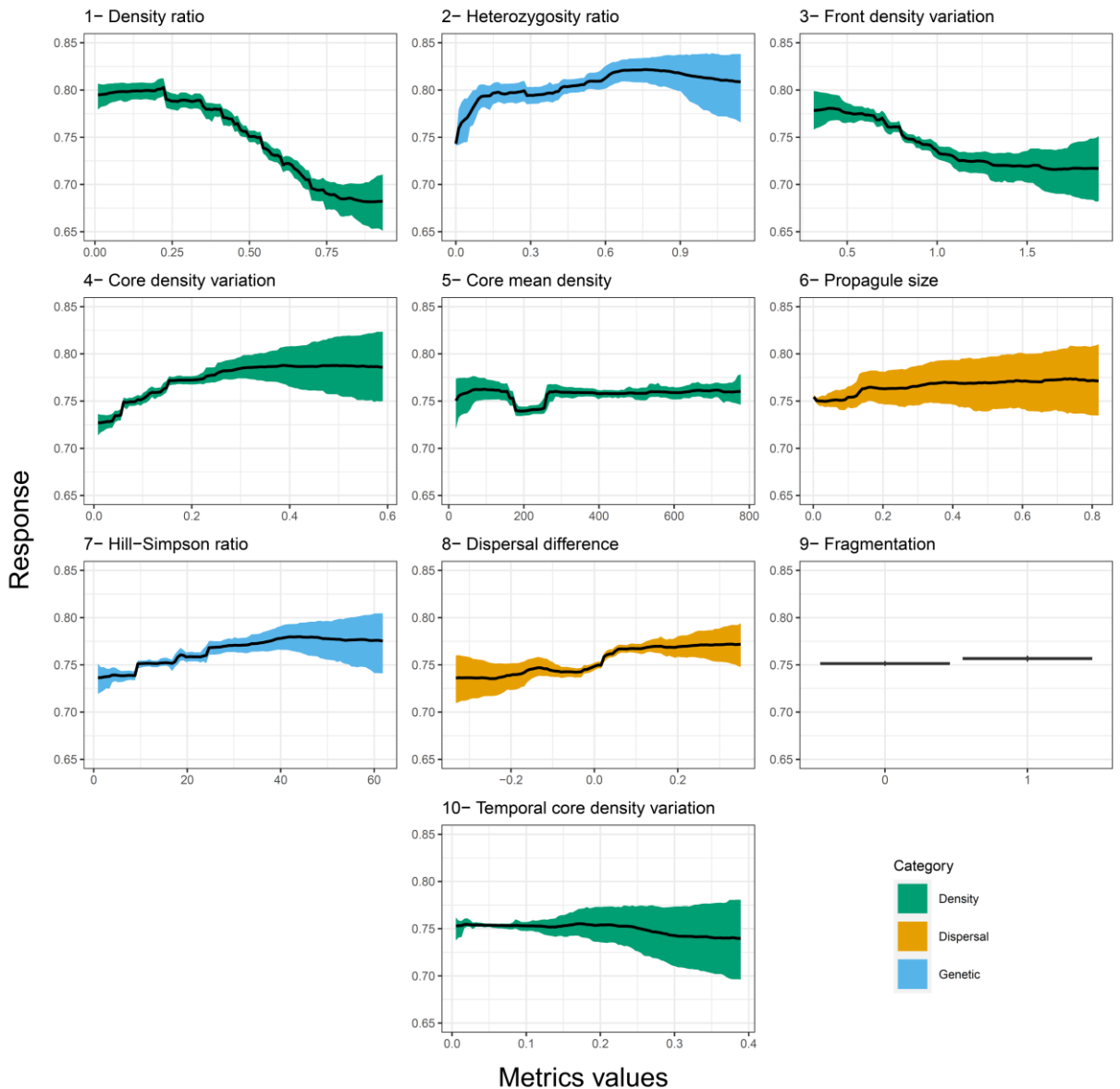
time they matched the expectations presented in [Table IV-2](#): Higher values of dispersal difference, Hill-Simpson index, heterozygosity ratio, propagule size with lower values of edge density variation tended to get higher values of allelic retention ([Figure IV.6](#)). The same can be observed for the presence of DDD+ ([Figure IV.5](#)). However, the density ratio and core density variation for predicting the allelic retention value showed opposite results. As for predicting the presence of DDD+, it was the mean core density that showed opposite results than expected.



**Figure IV.5: Metrics partial dependences of the DDD+ model fitted with the full metric set.**

Metrics are sorted from the most important in predicting the response value to the least important. The 95% credible intervals' colours represent the three different metric categories (related to genetic diversity, dispersal or density dynamics)

Allelic retention model partial dependences, in order of importance



**Figure IV.6: Metrics partial dependences of the allelic retention model fitted with the full metric set.**

Metrics are sorted from the most important in predicting the response value to the least important. The 95% credible intervals' colours represent the three different metric categories (related to genetic diversity, dispersal or density dynamics).

## Discussion

### *Promising model performances across various metrics of pushedness*

While no universal threshold exists for our measures of model performance, our models seem to perform generally well, especially knowing the huge intrinsic stochasticity present in the dynamics of expanding populations, which may present fundamental limits to predictability (Melbourne & Hastings, 2009). This is especially true since this study represents a first attempt at finding a relevant metric set. The encouraging performance when using variables specifically chosen based on ecological knowledge and existing theory on pushed and pulled waves and hypotheses (Bonnefon et al., 2013; Williams & Levine, 2018; Gandhi et al., 2019; Haond et al., 2021) is a first validation of the idea that a set of "weak" indicators might help determine the type of an expansion wave when "strong" direct knowledge is costly or impossible to obtain.

Interestingly, removing observed dispersal differences from the predictor set has little to no impact on our ability to predict allelic retention. At the same time, it decreases markedly our ability to predict DDD+ (**Figure IV.3**, **Figure IV.4**, **Table IV-3** and **Table IV-4**). We could have expected that excluding this metric would have a similar effect independently of the response since the underlying target process (pushedness) is the same. This is plainly not the case. On the one hand, those results confirm our assumption that the dispersal difference is an important predictor of the presence of DDD+ because it can be seen as merely a noisy measurement of it (see the threshold response **Figure IV.5**).

On the other hand, while neutral genetic diversity, measured through allelic retention, does vary with density-dependent dispersal as expected from theory (Birzu et al., 2019), **Figure IV.6**), our dispersal difference metric is a much weaker predictor of it (**Figure IV.5**, **Figure IV.6**, **Table IV-3** and **Table IV-4**). This highlights first that when individual stochasticity is included, the relationship between density-dependent dispersal may be less evident or much noisier than expected from theory, as seen in **Appendix 1**. Second, the underlying causal path linking genetic diversity to density-dependence can reasonably be summed up as density-dependent dispersal having demographic consequences that then lead to genetic diversity variation. In that context, if demographic data are available,

one may not need detailed knowledge about dispersal to predict genetic diversity (Willi et al., 2020; Peres & Mantelatto, 2023, but see Buffalo, 2021). One key question scientists attempting to predict pushed vs. pulled expansions will, therefore, need to ask is: are they attempting to predict the mechanism (DDD+ in our case) or its consequences (allelic retention here)? Our results show that the most relevant metrics may differ in either case.

*Most variables varied according to the expectations from the pulled vs. pushed theory.*

Detailed sensitivity analyses are needed to quantify each metric's marginal effects and identify redundant variables (Saltelli, 2002). Still, when it was possible to observe a variation between low and high values for one metric (no flat slopes), we found most of the time the expected result on pushedness: for example, a high dispersal difference between core and edge patches was associated with higher probabilities to having the presence of positive density-dependent dispersal, but also with higher allelic retention, two signs of more pushed expansion (Bonnefon et al., 2013; Birzu et al., 2019; Zhu et al., 2023). We also observed an increase in propagule size for more pushed responses' values as more individuals are needed to colonise a new patch (Williams & Levine, 2018) and a higher heterozygosity ratio between core and edge patches, representative of higher conservation of neutral genetic diversity over the entirety of pushed expansions (Bonnefon et al., 2013; Gandhi et al., 2019).

On the contrary, the density ratio and mean core variance follow expectations for DDD+ but have opposed results for allelic diversity, with a higher ratio and lower mean core variance leading to lower allelic retention (**Figure IV.6**). An opposing result is also present for predicting DDD+, with lower mean core densities in pushed expansions (**Figure IV.5**). As discussed above, those contrasted results highlight how our expectations are highly dependent on the response and that two different stories can be told inside the same expansion, based on which aspect (genetic or dispersal) is the focus, even when DDD+ and spatial genetic diversity are linked (Roques et al., 2012; Birzu et al., 2018, 2021).

*Sub-datasets' varying levels of predictive power may reflect an additional category: locked expansions.*

Although, as we've seen, models on DDD+ and allelic regression behave very differently in many ways, their performance seems to vary very consistently depending on specific sub-sections of the training dataset, with better predictive performance on high fecundity or low dispersal mortality subsets, across the board (**Table IV-4**).

Interestingly, the expansion scenarios on which our models performed worse (low fecundity/high mortality) were also less likely to expand regularly. First, they match the scenarios in which extinctions and expansion failures were more likely in the detailed study **Appendix 1**. Second, they also match the scenarios in the present study in which no expansion occurred during the last five generations (see Methods). While further analysis is needed, some of these pushed expansions may be closer to pinned or locked expansions, as in Wang et al. (2019). While pinned expansions stop expanding and stay stuck at one edge patch, locked expansions continue to advance but with a pulsed rhythm and regular progress stops. Pinned or slower expansions can also arise from landscapes with gaps (Urquhart & Williams, 2021; Morel-Journel et al., 2022), which are in part abstracted into high dispersal mortality in our model. Range locking or near-range pinning might be why models' performances are lower for those two sub-datasets, as some replicates are actually outside the pushed/pulled continuum. We might end up having to develop trinary rather than binary classification models (pulled/pushed/locked), to be able to predict the frequency of pushed expansions accurately.

*Further perspectives: what to predict, how to predict it*

While our results here are promising, they are a first step in a larger plan. In the long term, we hope that using a set of easy-to-get metrics can become a reliable tool to predict the placement of actual expansions on the pushed/pulled continuum. However, to get to that point, there are still many areas where further work is needed. First, we know that Allee effects can also generate pushed dynamics (Roques et al., 2012; Gandhi et al., 2016; Erm & Phillips, 2020). To be fit for purpose, our predictive framework needs to be able to predict pushed expansions irrespective of the exact mechanism generating the underlying density-dependence and, therefore, to include both simulated expansions with density-

dependent dispersal and with Allee effects in its training set. An open question is whether different types of pushed expansions can be predicted by the same metrics (i.e. if there is a common demographic or genetic signature of pushedness), or whether one would need to predict the probability that expansions are pushed for each mechanism separately. Second, further analyses may help us refine our set of predictor metrics, for instance, by casting aside metrics that are both weak predictors and harder to collect in natural scenarios. In our current set, this includes temporal variation in core density, which is the least important for both DDD+ and allelic retention models ([Figure IV.5](#), [Figure IV.6](#)) and a metric that needs longitudinal surveys across several generations to be estimated.

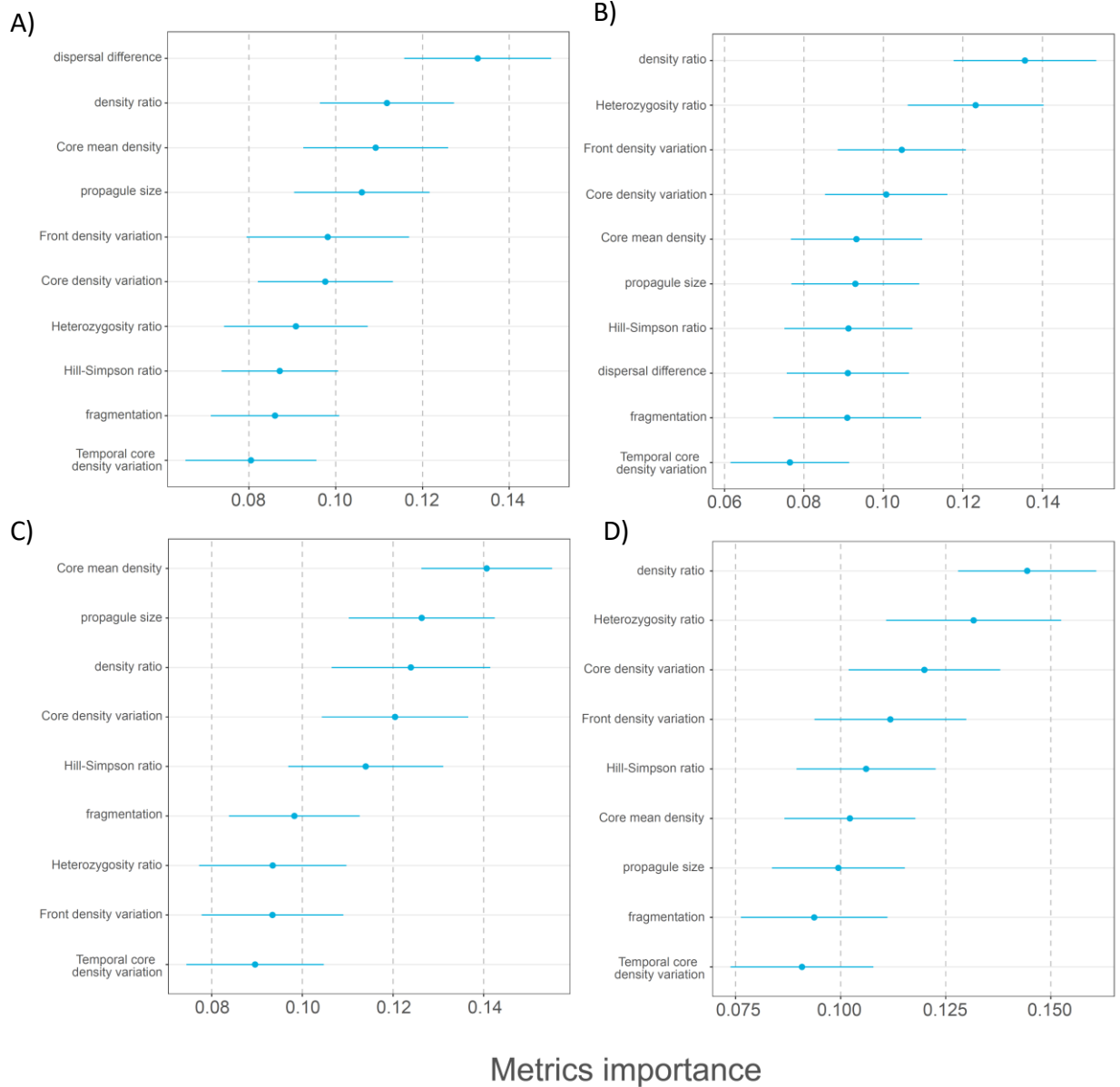
Finally, the simulated expansions used to train our predictors will need to be much more realistic than in our current simplistic "toy" model for an application to natural expansions. This includes more realistic modelling of the focal species traits on one side and local geographical and environmental conditions on the other. While developing such a tailor-made platform from scratch is an option, the RangeShifter modelling framework and its recent revamp (Bocedi et al., 2021), among others, already provide most, if not all, the tools needed to generate precisely the kind of realistic simulations needed for the application of our predictive framework.



## Article 4: Supplementary Materials

### Supplementary Materials 1: More details on metrics importance

In [Figure IV.5](#) and [Figure IV.6](#) of the main paper, metrics are sorted by importance to correctly predict the model response category or value. The order was determined using the `varimp()` function of the *embarcadero* package (version 1.2.0.1003) (Carlson, 2020). The importance was measured using the proportion of total branches used, and error bars represent the standard deviation. The close proximity of some metrics' importance shows that the order change for some metrics in the paper is not from a large margin difference and more because they have qualitatively the same importance.

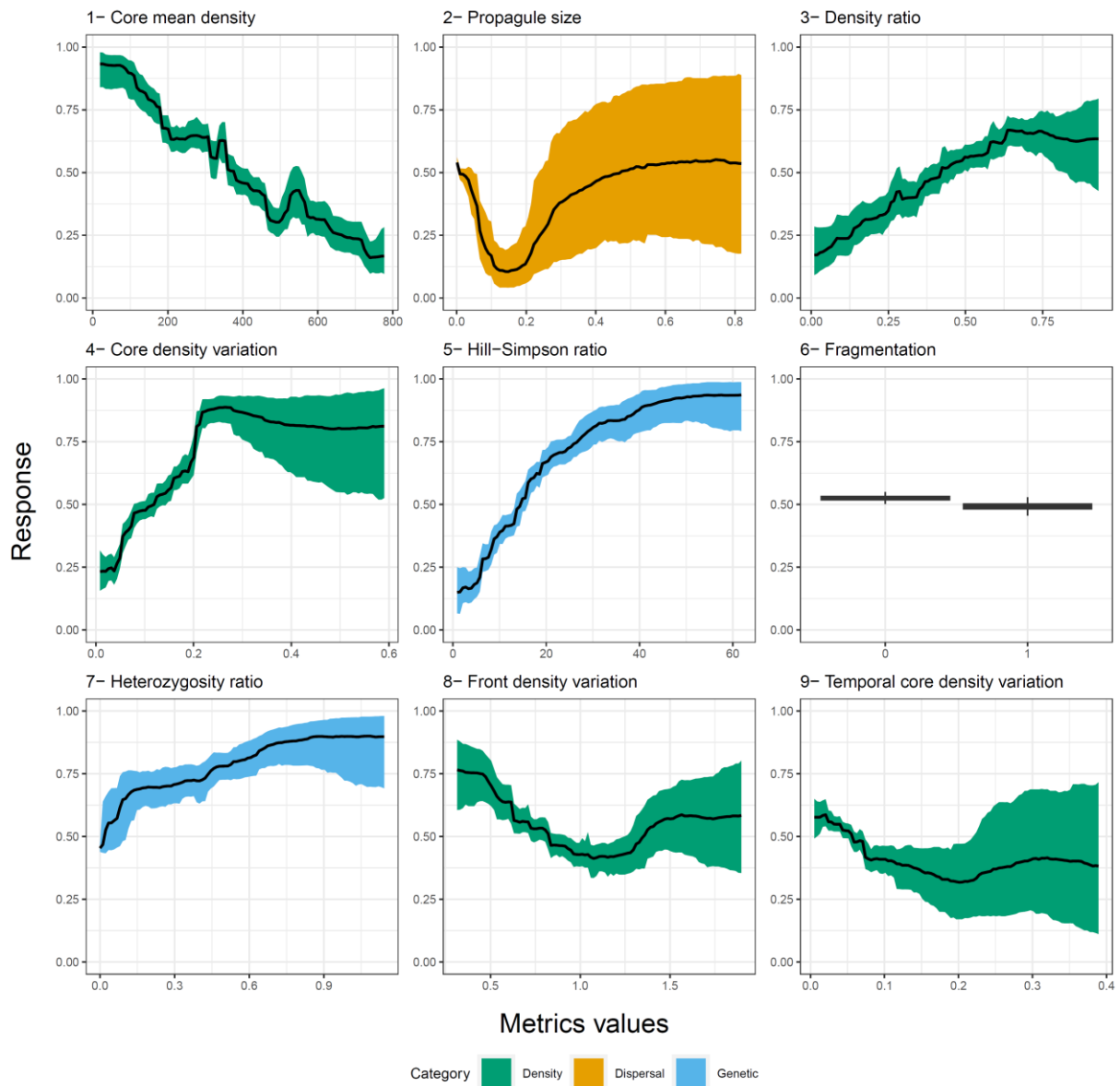


**Supplementary Figure IV.1: Precise metric importance classification**

A) DDD+ response, fitted on full metric set; B) Allelic retention response, fitted on full metric set;  
 C) DDD+ response, fitted on partial metric set; D) Allelic retention, fitted on partial metric set.

## Supplementary Materials 2: Partial dependence plots for the partial metric set

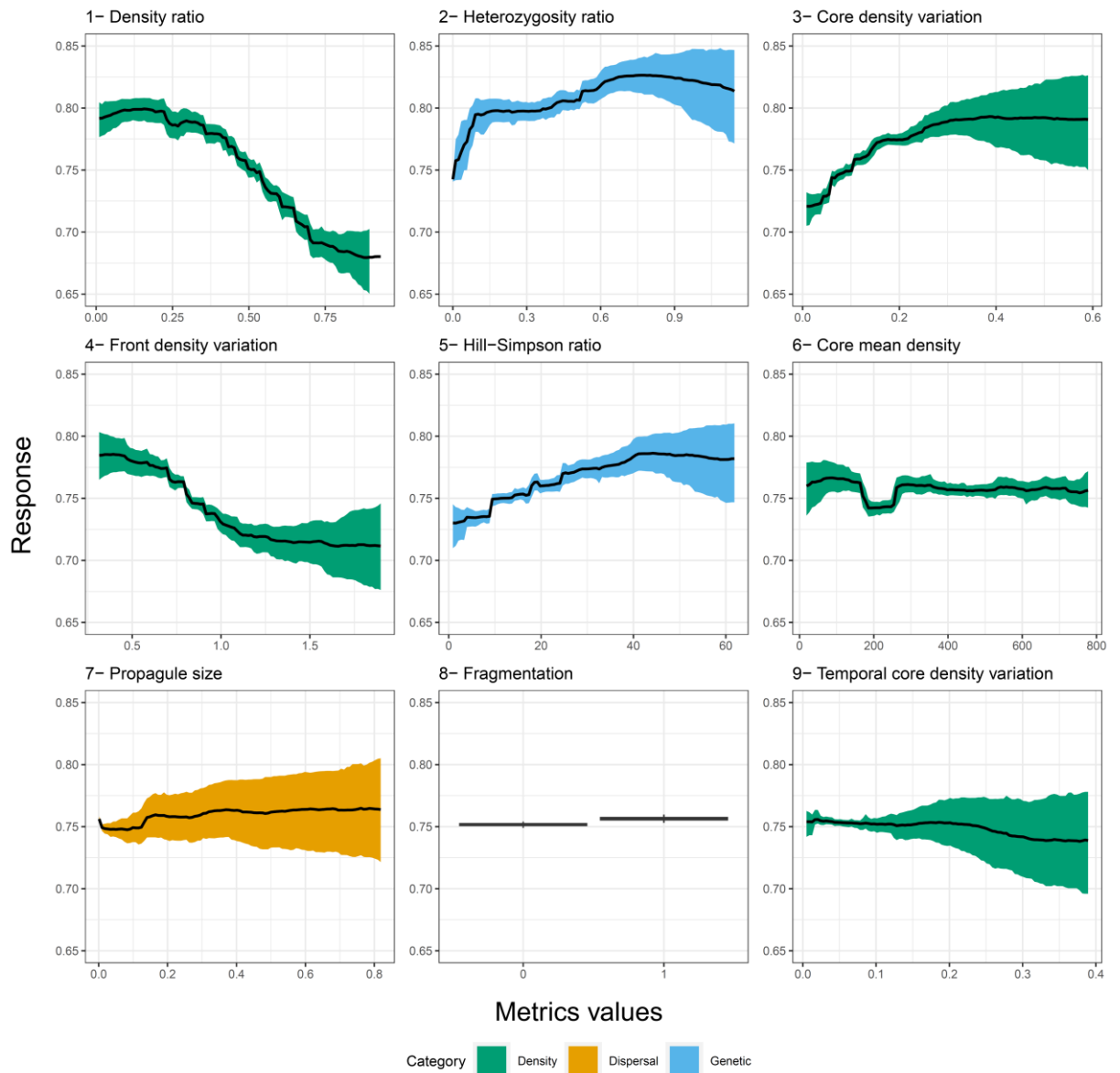
DDD minus dispdiff model partial dependences, in order of importance



**Supplementary Figure IV.2: Metrics partial dependences of the DDD+ model fitted with the partial metric set.**

Metrics are sorted from the most important in predicting the response value to the least important. The 95% credible intervals' colours represent the three different metric categories (related to genetic diversity, dispersal or density dynamics).

Allelic retention minus dispdiff model partial dependences, in order of importance



**Supplementary Figure IV.3: Metrics partial dependences of the allelic retention model fitted with the partial metric set.**

Metrics are sorted from the most important in predicting the response value to the least important. The 95% credible intervals' colours represent the three different metric categories (related to genetic diversity, dispersal or density dynamics).

**To sum up :**

- Our models presented promising predictive power about the presence of positive density-dependence in dispersal and the spatial measure of genetic diversity, the allelic retention
- The predictive power was still good when the measure of differences in dispersal rates between core and front (a nearly direct measure of positive density-dependence in dispersal) was removed from the metric set
- Depending on the response studied, a shift in variable importance is observed, linked to the nature of the response variable (more linked to neutral genetic diversity or dispersal abilities)
- The decrease in predictive power under particular scenarios could be explained by more pinned expansions dynamics, falling outside of pushed/pulled expectations.

V- General discussion: what did we get,  
what can we do, what is next?

Population expansions are increasingly common, whether driven by an intensification of human transportation around the globe without careful control of potential stowaways or environmental shifts (mainly resulting from climate change). More and more research suggest we need to account for the complexity of eco-evolutionary dynamics to manage population expansions.

One of the goals of this thesis is to explore these eco-evolutionary dynamics within pushed/pulled expansions and how negative trait correlation could influence said dynamics. I first explored the many intra- and interspecific trait variations in *Trichogramma* wasps to understand how it was structured, particularly whether it exhibited a pace-of-life axis ([Chapter II-](#), Article 1). This comparative analysis helped me to design experimental expansions to observe how the pace-of-life axis could affect pushed/pulled dynamics ([Chapter II-](#), Article 2). I then used simulated expansions to observe the influence of trait correlation and evolution of dispersal traits on the global eco-evolutionary processes of initial pushed or pulled expansions ([Chapter III-](#), Article 3). Finally, I developed a prototype method to detect pushedness (or at least the presence of positive density-dependence and one neutral genetic diversity pattern that can be generated through pushed dynamics) from a demographic and genetic metrics relatively easy to collect in the field ([Chapter IV-](#), Article 4).

## Linking pace-of-life theory and pushed/pulled continuum: Slower populations for more pushed expansions?

### Slower life histories generate more pushed demographic dynamics

During chapter II of this thesis, we found that the five species of *Trichogramma* presented an interspecific negative correlation between reproduction and development time (Article 1). This negative correlation between two life-history traits represents one of the axes used to define the pace of life (Bielby et al., 2007; Gaillard et al., 2016). We were able to classify our five studied species from slowest to fastest: *T. bourarachae*, *T. evanescens*, *T. principium*, *T. semblidis* and *T. brassicae*, with no similar axes found within species, among lines. This structuration of life history along a major axis offered the possibility to

test hypotheses on the link between pushed/pulled species expansion dynamics and slow/fast history. In Article 2, we found that the slowest species, *T. bourarachae*, tended toward partial ecological dynamics similar to the ones generated by pushed expansions, while the fastest, *T. brassicae*, had more pulled-like tendencies.

As discussed in the introduction, one common theory is that as conspecific densities decrease along the expansion front, the pressure it imposes through intraspecific competition also decreases, and we expect to observe *r*-selection at the leading edge (Phillips, 2009; Burton et al., 2010). On the contrary, the higher conspecific pressure behind the leading edge results in a selection toward competition resistance, or *K*-selection. This key expectation was recovered in results from the next article, which explored the influence of a competition-colonisation trade-off on expansion dynamics (Article 3). There are links between the concepts of *r*-*K* selection and pace-of-life theory, and the latter can be considered a precursor or special case of the latter (Jeschke & Kokko, 2009); in the context of range expansion, we should expect slow paces favouring *K*-selection, therefore more present at the range core, and fast paces favouring *r*-selection at the leading edge.

Our results here extend and complete these ideas about the pace of life and the density pattern during expansion by exploring the whole eco-evolutionary feedback: the pace of life, representing traits (co)evolutionary history, influences density patterns by generating more pushed or pulled expansions, and those density patterns alter traits (co)evolution, as seen by the differing changes in phenotypic traits values between species (Article 2). This link between pace of life and initial expansion dynamics may be related to the probability of generating positive density dependence within populations. In slow populations, maximising the resistance to intra-specific competition (or increasing cooperation) may decrease the *per capita* growth rate at low densities because of trade-offs (Ribeiro, 2015). The question of the link between this slow axis and higher probabilities of positive density dependence in dispersal is more complicated, as while dispersal has often been linked to life history (Réale et al., 2010; Stevens et al., 2012, 2013; Wright et al., 2019), this is not always the case (i.e. in Article 1). Our simulation results in Article 3 suggest that even when the structure of life history/the pace of life does shape dispersal, it may not actually lead to changes in density-dependent dispersal. This suggests



that the correlation between pace of life and expansions modulated by positive density-dependence in dispersal may depend on which dispersal trait is allowed to evolve.

For now, I have shown that the pace of life may shape expansion dynamics of experimental *Trichogramma* populations, but was not able to show that this shaped trait evolution in turn. To reconcile experiment and simulation results, an idea would be to use our experimental data to parametrise (an expanded version of) the model. Rather than generating replicates with similar average traits but varying correlation, future simulation studies could, as in the experiment, compare expansion dynamics of populations with initially slower or faster life histories.

## Discussing the possible influence of sex ratio on pushed/pulled dynamics

A key life history dimension we did not explore in this thesis is sex ratio. As many haplo-diploid arthropods, *Trichogramma* females should be able to control the proportion of males (unfertilised eggs) and females (fertilised eggs) in their progeny, therefore able to adjust the ratio between the two to optimise their fitness, as proposed in the concept of Local Male Competition (Hamilton, 1967; Taylor & Bulmer, 1980). The Local Male Competition concept suggests that in an environment with isolated patches colonised by fertilised females, a unique foundress will have offsprings with a sex ratio biased toward females, with just enough males to fertilise all daughters, as female offsprings have the highest fitness value. As the number of foundresses increases, related male competition decreases, and we observe more male offsprings per female (observed e.g. in Luck et al., 2001; Macke et al., 2012). We also know that in *Trichogramma evanescens*, the population sex ratio changes with parasitoid density (Waage & Lane, 1984), but this response may depend on the species observed (Martel & Boivin, 2004).

Because the sex ratio can have direct consequences on the genetic drift, overall evolution of small populations through effective population size (Nomura, 2002), and even lead to extinctions (Lee et al., 2011), we can wonder if the sex ratio varies with density in our case, if this variation is similar between the different species, and if it can influence the expansion dynamic observed. For instance, we could observe sex-biased dispersal

(Trochet et al., 2016; Li & Kokko, 2019), sex-biased dispersal syndromes (Mishra et al., 2018) or even sex-specific pace-of-life syndromes (Immonen et al., 2018) within our populations. A first study of the specimens collected during the experimental expansion at different times and locations can be combined with our results to explore the relationship between demographic expansion dynamics and the sex ratio.

## Analyses of the genetic data collected during expansion experiments to complete our knowledge about the link between life history and pushed/pulled dynamics

While we only analysed experimental data at a demographic level, we know that pushed/pulled expansions are expected to vary on a genetic level (Roques et al., 2012; Bonnefon et al., 2013, 2014; Birzu et al., 2019, 2021). We demonstrated in our simulations that even in the presence of trait correlation, expansions with initial positive density dependence retain higher neutral genetic diversity (Article 3). However, we found that the link between density dependence and genetic diversity is not fixed and can be altered by environmental factors, such as dispersal costs ([Appendix 1](#)). In addition, in Article 4, genetic metrics present within the set are overall not the most important to predict positive density-dependence in dispersal. Altogether, our results challenge the common assumption (Roques et al., 2012; Birzu et al., 2019) that pushed dynamics and higher genetic diversity are synonymous and point to the need for more realism in theoretical studies of pushedness.

Our results on simulated expansions, previous mismatches, and theoretical predictions could help us decide on the best approach to analyse the genetic data collected during the expansion experiments. Indeed, we extracted pooled samples of different replicates at the experiment's start (initial population) and the end (at range core and range edge). We could look at how the presence of a pace of life and consequent variation in life history trait values between species may influence expected patterns. While we observed in Article 3 that there is no influences of trait correlation on genetic diversity, we looked at the effect of the correlation strength, not the position within the pace-of-life axis. Based on common assumptions, the expectation is that if slower replicates generate more

pushed expansions, a comparatively lower genetic diversity loss should also be observed. However, we also know that the life-history strategies may influence by itself genetic diversity, with long-lived/low-fecundity species presenting less genetic diversity (albeit not in an expansion context, Romiguier et al., 2014) and could modify the expected correlation. The future expanded version of our model mentioned above could help us predict the links between diversity patterns and the initial population's position within the pace of life. These predictions could then be tested using the collected data.

To get further, we may expect pushed/pulled dynamics can affect the adaptive potential of an expanding population, i.e. the capacity to adapt to environmental changes. First, population sizes shape adaptive potential (Willi et al., 2006; Hoffmann et al., 2017), and second, we know that pulled expansions will tend to result in more successive low-density patches at the front than pushed expansions (Williams & Levine, 2018; Haond et al., 2021; to some extent Articles 2 and 4). If a clear link between pushed/pulled dynamics and adaptive potential is found, then determining the pushedness of expansions in the wild gets even more interesting, as it may help us make the best management decisions (but see Jiang et al., 2023). The availability of genomic resources from our *Trichogramma* experiments means we have an unprecedented opportunity to explore the influence of pushed/pulled expansions on the adaptive potential. By comparing the relative frequencies of mutations, we could explore which parts of the genome are under positive, negative selection or gene surfing (Stinchcombe et al., 2017) and if there is a variation depending on the expansion dynamic or initial pace-of-life position. Afterwards, annotated reference genomes could help us explore the functional aspect of regions under selection.

## More about eco-evolutionary dynamics and feedbacks

### The importance of individual-level variation to pushed/pulled dynamics

We demonstrated in [Appendix 1](#) that individual variation in dispersal traits and their evolution can result in a shift in expansion dynamics. While some scenarios gave results

similar to Erm & Phillips (2020), with expansions becoming more pulled with time, most of them tended to maintain a pushed dynamic, with even the possibility of initially pulled expansions becoming more pushed.

We did observe phenotypic evolution in our experiments (Article 2), namely the shift from positive density-dependence in overall fecundity to negative density-dependence at the front for the slowest species, *T. bourarachae*. This shift is an indicator of the pushed expansion becoming more pulled with time, at least at the leading edge, matching with Erm & Phillips (2020). However, our experiment's restricted number of generations does not allow us to observe the potential complete cycle of eco-evolutionary feedbacks and determine if this shift from pushed to pulled is permanent or transitory in the leading edge.

Interestingly, our results, when compared to the literature, suggest that in the presence of evolution, the trajectories taken by expansions will depend on the mechanism generating positive density dependence. Allee-generated pushed expansions shifted to become more pulled (Erm & Phillips, 2020), while positive density-dependent dispersal-generated pushed expansions became, in most situations, more pushed ([Appendix 1](#)). However, this remains a comparison between two different studies with different protocols. The simplest way to determine whether or not Allee effects and dispersal have qualitatively different consequences would be to use one singular Individual-Based Model to generate expansions where density-dependence in dispersal and/or growth could evolve under similar conditions and observe the evolutionary trajectories. If such a study confirmed these differences, this would again add complexity in a theory where density-dependence in growth and dispersal were thought to be interchangeable (Birzu et al., 2019) and might make the development of operational "generalized pushedness detectors" (see below) harder.

## The role of abiotic factors

We did not compare different abiotic conditions in the experimental and most simulated expansions (Article 2 and 3). However, we know that outside of pushed/pulled theory, habitat fragmentation (Jacquemyn et al., 2012; Cote et al., 2017; Urquhart & Williams,

2021), dispersal costs (Travis et al., 1999; Rousset & Gandon, 2002), or even environmental fluctuation (Friedenberg, 2003) can have an effect on evolution during expansions. Results from [Appendix 1](#) demonstrated the importance of dispersal costs in influencing evolutionary trajectories. Only when dispersal costs were low did we observe an evolution toward an overall decrease in density-dependent dispersal in some scenarios, therefore, more pulled expansion. These simulation results show that external factors are another source of selective pressure and should be accounted for in the future study about the evolution of pulled versus pushed expansions proposed above.

## First steps towards functional detectors of pushedness in the field

### A first encouraging proof of concept about exploiting easy metrics set

Our proof of concept in Article 4 shows that detecting pushedness from typical field data is feasible in principle. Even though various sources of variation and stochasticity were added within the datasets (by compiling different values of growth rate, carrying capacity, juvenile survival, dispersal cost and dispersal rates at low density), our models did better than random chance. There are several ways in which this concept can be refined and tested on more complex expansions.

First, we saw that models performed better under some scenarios (higher fecundity or no dispersal costs) than others. We hypothesised that poorer performance could result from another kind of expansion dynamics: pinned and locked expansions (Wang et al., 2019; Morel-Journel et al., 2022). While our method is developed with the idea of predicting where an expansion is on a pushed/pulled continuum (or pushed/pulled dichotomy when looking at the presence of density-dependence in dispersal), an efficient tool may need to account in one way or another for the possibility that expansions can be neither pulled nor pushed but pinned or locked.

Second, we must remember that right now, the simulated expansions used in our "pushedness detector" do not include the potential shifts from pushed to pulled and vice versa caused by evolution (Erm & Phillips, 2020, [Appendix 1](#)). Without refinements to account for evolution, any predictor is bound to become increasingly inaccurate in many cases as the target expansion becomes increasingly older. The evolution of pushed/pulled dynamics during the expansion can make it harder to predict the future of an expansion (Williams et al., 2019), even more so at the leading edge where stochasticity is important (Weiss-Lehman et al., 2017, 2019). Thankfully, modelling frameworks such as RangeShifter (Bocedi et al., 2014, 2021) can also include realistic evolutionary dynamics (at least for dispersal), which means it should be possible, if not necessarily simple, to extend our prototype to account for these.

## Could we integrate life-history traits into the set?

On a related point, we showed in Article 2 that life-history traits seems to influence the position on pushed/pulled expansions. If it is possible to indirectly predict a population's positive density-dependence in dispersal or growth by looking at some traits shared with other populations that have known positive density-dependence, we could include said traits' values within our metric set to predict positive density-dependence and indirectly pushedness. The increasing availability of trait databases (e.g. Salguero-Gómez et al., 2015; Salguero-Gómez et al., 2016; Kattge et al., 2020) and synthetic datasets on the presence of density dependence may help in this (e.g. Kramer et al., 2009; Harman et al., 2020). To test this idea with our model, we can extract trait values from simulated expansions, add them to our metric set, and look at the partial dependence plots afterwards. Separating metrics into subsets will also help us determine how good predictions are when we only have partial information, like only life-history traits values, or only density metrics.

## Any last word? Broader openings in natural expansion management

During this thesis, I focused on the influence of density-dependence evolution in the context of pulled versus pushed expansions. It stands to reason that this evolution and subsequent shift in dynamics can be linked to other fields of study. As discussed previously, multiple genetic, demographic and evolutionary dynamics are influenced by how pushed an expansion is.

It opens the door for multiple questions about integrating pushed/pulled dynamics within management plans, with the possibility of going beyond exploiting Allee effects to limit population growth rate, such as the Slow The Spread Program against the spongy moth in the United States (Coleman & Liebhold, 2023). Beyond our focus on the mechanisms behind more pulled or pushed expansions, we can dig deeper into the ecological and evolutionary consequences of said expansions. Szűcs et al. (2019) reviewed predictions about the effects of rapid eco-evolutionary processes for biological control including the loss of genetic diversity, risks of expansion load and differential evolution at the leading edge. However, they highlighted that all their predictions were made within the classical framework of pulled-like expansions and expected that pushed expansions could limit those processes.

For instance, some proposed management methods use edited genes spreading into a population to limit various pathogen's propagation, as presented in Gantz et al. (2015) against malaria, by modifying populations of its vector, the mosquito *Anopheles stephensi*. However, gene drives need to be carefully controlled as it may result in irreversible transformations within wild populations. Tanaka et al. (2017) proposed a selective disadvantage range for the gene drive to generate pushed expansions within wild populations, limiting the accidental propagation outward, or allowing for an easier control of gene drive populations. The strategy of "genetic backburn", i.e. the introduction of individuals from the core populations ahead of the leading edge and near a landscape barrier in order to prevent high dispersers within said edge to attain and go over the landscape barrier (see Phillips et al., 2016), might see its efficiency vary between pushed

and pulled dynamics. Indeed, it relies in phenotypic variations between range core and edge, much more contrasted in pulled expansions than pushed ones, therefore potentially more efficient.

Overall, depending on the context in which an expansion happens, the management plan might have to be adapted to the pushed/pulled dynamics and highlights the need to be able to determine the nature of an expansion, or to know how to modify the pushedness in order to optimise the selected strategy.





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## VII- Appendix

### Appendix 1: Individual variation in dispersal shapes the fate of pushed vs. pulled range expansions

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#### Abstract

Ecological and evolutionary dynamics of range expansions are shaped by both dispersal and population growth. Accordingly, density-dependence in either dispersal or growth determines whether expansions are pulled or pushed, i.e. whether spread is mainly driven by recent, low-density edge populations, or by older populations closer to the core. Despite this and abundant evidence of dispersal evolution during expansions, the impact of density-dependent dispersal and its evolution on these expansion dynamics remains understudied. Here, we used individual-based simulations to examine how individual trait variation in both maximum dispersal rate and dispersal density-dependence shapes expansions and their position on the pulled-pushed continuum. We found that in the absence of evolution, dispersal costs greatly influence internal dynamics during expansions, to the point they may dampen the fundamental positive relationship between density-dependence and genetic diversity expected from pushed expansion theory. Non-heritable variation in traits has no meaningful effect on that relationship. By contrast, heritable variation in traits linked to density-dependence, and the resulting evolutionary dynamics at the range edge, can preserve a positive relationship between density-dependence and genetic diversity even when dispersal costs are high. Examining evolutionary changes in traits in more detail shows that dispersal at the range front evolved towards trait combinations associated with more pushed expansions across most contexts, with combinations linked to more pulled expansions only favoured when costs are low, and even then only under some scenarios. More generally, our results show that both phenotypic evolution and environmental context (here dispersal costs) can interact to reshape fundamental aspects of pushed vs. pulled expansions, and that environmental context can have major impacts even in the absence of evolution or phenotypic variation. Those simulations suggest new avenues of research to explore, both in terms of theoretical studies and regarding ways to empirically study pushed vs. pulled range expansions.

**Keywords:** density-dependent dispersal; dispersal evolution; individual-based models; genetic diversity; heritability



## Introduction

By redistributing genes and individuals in space, often non-randomly, dispersal has the potential to influence many aspects of ecological dynamics (Clobert et al. 2012; Jacob et al. 2019; Raffard et al. 2021). Understanding what drives dispersal is especially important in the context of range expansions and climate-driven range shifts, as spread in space is the direct product of both dispersal and population growth dynamics (Lewis et al. 2016). Dispersal is a complex trait with multiple and interacting drivers (Bowler and Benton 2005; Matthysen 2012). Intuitively, one may assume that qualitatively different dispersal or growth functions would therefore lead to qualitatively different expansion dynamics. In the context of range expansions, this has been especially studied with respect to density-dependence. One can indeed differentiate between so-called "pulled" or "pushed" expansions based on the density-dependence of population growth and/or dispersal (Stokes 1976; Lewis et al. 2016; Gandhi et al. 2016; Birzu et al. 2019). On the one hand, pulled expansions are typically expected when growth is maximal at low densities and dispersal is density-independent; spatial spread is then primarily driven by what happens in the low-density, newly founded edge populations. On the other hand, pushed expansions can happen when dispersal and/or growth are instead increasing with population density, due to positive density-dependent dispersal or demographic Allee effects (Birzu et al. 2019). In that case, the contributions of dispersal and growth at the low-density edge to overall spread can be outweighed by what happens in older more densely populated habitats; expansions are thus "pushed" forward by these older populations. While mathematical studies have often assumed or demonstrated a qualitative distinction between pushed and pulled expansions (Lewis et al. 2016), recent works suggest that it may be more practical for ecologists and evolutionary biologists to see "pushiness" as a continuum. First, some theoretical studies have described "semi-pushed" expansions that bridge the gap between strictly pushed and pulled expansions at intermediate levels of density-dependence (Birzu et al. 2018, 2019). Second, many ecological and evolutionary properties of interest actually change gradually as density-dependence increases, even within the range of pushed expansions *stricto sensu* (Gandhi et al. 2016, 2019; Birzu et al. 2018, 2019; Zhu et al. 2023).

Pushed expansions differ from pulled expansions in many aspects such as population genetics, relative expansion speed, population sizes at the range edge... (Roques et al. 2012; Lewis et al. 2016; Gandhi et al. 2016; Birzu et al. 2019). In particular, the pushed or pulled nature of an expansion is expected to have major effects on the underlying evolutionary dynamics (summarized in Miller et al. 2020): a key property of (more) pushed expansions is that they should lose genetic diversity at the expanding edge slower than (more) pulled ones, if at all (Roques et al. 2012; Birzu et al. 2019; Gandhi et al. 2019). On the one side, higher genetic diversity in pushed expansions may mean they are better equipped to successfully adapt to new environmental conditions encountered during expansion (Szűcs et al. 2017a). On the other hand, the fact that founding population sizes may be larger at the edge in pushed expansions may mean that spatial sorting processes (Phillips and Perkins 2019 and see below) are less selective (Miller et al. 2020).

Interestingly, the traditional view of the pushed/pulled expansion distinction in theoretical works implicitly assumes there is no individual variation, and thus no evolution, in the very traits that generate "pushiness" itself; that is, the density-dispersal and density-growth functions are the same for all individuals, and remain constant during the expansion (e.g. Stokes 1976; Roques et al. 2012; Lewis et al. 2016; Birzu et al. 2018, 2019; for a notable exception, see Erm and Phillips 2020). However, individual variation in dispersal and dispersal-related traits is actually very common and now well documented (Bowler and Benton 2005; Ronce and Clobert 2012; Cote et al. 2017), and while a lot of questions remain, it is clear that this variation is often at least partly genetic (Saastamoinen et al. 2018). Following Cote et al. (2017)'s terminology, we can distinguish individual variation in dispersal capacity/ability from individual variation in context-dependence. Variation in dispersal ability will be driven by variation in either "enabling traits", which make dispersal possible at all (e.g. presence/ absence of wings, Simmons and Thomas 2004) or in "enhancing traits" which make it easier/ more efficient, such as e.g. body size or wing/leg length (Cote et al. 2022). Variation in dispersal context-dependence can be linked to "matching traits" that lead to non-random dispersal in response to experienced environmental conditions (Edelaar et al. 2019; e.g. Jacob et al. 2019; Cote et al. 2022).

We also know that this individual variation can influence spread dynamics during range expansions (Miller et al. 2020). Genetic differences in dispersal traits can fuel evolution at the expanding range edge by spatial sorting, as at each generation, individuals with spread-facilitating traits are more likely to advance to new habitats and reproduce there (Shine et al. 2011; Phillips and Perkins 2019). The effects of spatial sorting on spread velocity are well documented, thanks in particular to iconic natural examples (e.g. Phillips et al. 2006) and experiments where researchers reshuffle individuals in space to cancel out the effects of spatial evolution (Ochocki and Miller 2017; Weiss-Lehman et al. 2017). Because dispersal is often associated with other traits in syndromes (Ronce and Clobert 2012), changes in many traits along expansions are potentially linked with spatial sorting (Chuang and Peterson 2016).

Despite indications that not only dispersal capacity, but also dispersal density-dependence itself may evolve during range expansions (Travis et al. 2009; Fronhofer et al. 2017; Weiss-Lehman et al. 2017; Mishra et al. 2020; Dahirel et al. 2021), we don't know how the structure of individual variation in dispersal influences pushed/pulled expansion dynamics, or vice-versa. Indeed, the one theoretical study so far on the evolution of pushed/pulled dynamics, which showed that genetic variation leads pushed expansions to become pulled with time, was focused on Allee effects only (Erm and Phillips 2020). In the context of dispersal but outside of the pushed expansion framework, it has been shown that dispersal can become more consistently high across a broad range of densities during expansions, compared to stationary meta-populations (Travis et al. 2009). This may or may not agree with Erm and Phillips (2020)'s predictions, depending on whether dispersal becomes truly density-independent in expansions or whether some positive density-dependence remains at the lowest densities. Furthermore, that theoretical study and others typically use dispersal functions that only allow only positive density-dependent dispersal to evolve (Travis et al. 2009; Hovestadt et al. 2010), even though negative density-dependent dispersal is common in nature (Harman et al. 2020). This may explain mismatches with some of the few existing experimental studies (Fronhofer et al. 2017; Mishra et al. 2020; Dahirel et al. 2021).

In this context, we used individual-based simulations to examine how genetic vs. non-genetic inter-individual trait variation influence the evolution and maintenance of (more)

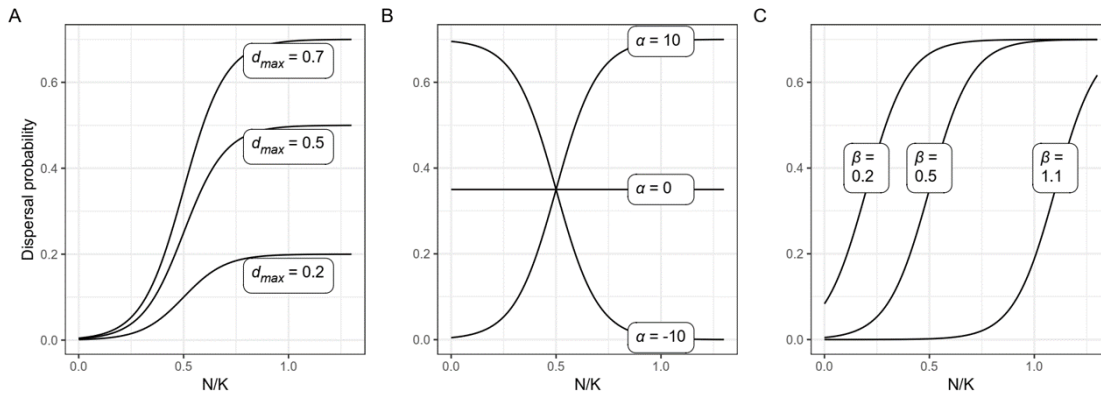
pushed vs (more) pulled expansion dynamics. We focused here on dispersal variation: positive density-dependent dispersal is very common (Harman et al. 2020), something that is not (yet) reflected in the literature on pushed expansions, which has mostly focused so far on Allee effects (for explicit exceptions, see Birzu et al. 2019; Wang et al. 2019). We simulated expansions varying in initial trait distribution and sources of variation (genetic and non-genetic variation in maximum dispersal rate, density-dependence, both or neither), and examined how this shaped dispersal traits, expansion speed and genetic diversity. We additionally analyzed how dispersal costs (Bonte et al. 2012) interact with these sources of variation to shape dispersal evolution and the relationship between density-dependence and genetic diversity during range expansions. In non-expanding populations at least, higher costs are predicted to favour more positive density-dependent dispersal (Travis et al. 1999; Rodrigues and Johnstone 2014), which would influence the evolution of pushed vs. pulled dynamics.

## Methods

We wrote a discrete-time and discrete-space simulation model in NetLogo (Wilensky 1999) version 6.2.0. We interacted with the model and designed our virtual experiments using the `nlr` R package (Salecker et al. 2019). We provide below a summarised description of the model, before presenting the simulation experiments we ran using it. A detailed description of the simulation model using the ODD protocol (Grimm et al. 2010; Grimm et al. 2020) can be found in **Supplementary Material S1**, and a copy is attached with the model and analysis code (**Data availability**).

### *Summarised model description*

The model simulates asexual haploid individuals spreading in a linear discrete landscape, with their growth dynamics shaped by a Ricker model and their dispersal by Kun and Scheuring (2006)'s model (**Fig. 1**). Dispersal and growth are both stochastic. Individuals can vary or not in traits shaping dispersal, and that variation can be more or less heritable. Dispersal is limited to the nearest neighbours, and dispersal costs can be imposed in the form of a mortality risk.



**Figure 1.** Illustration of the dispersal function used in the individual-based model (based on Kun and Scheuring 2006) and some of its properties. Each panel shows the effect of changing one of the three underlying variables while keeping the other two constant (values when kept constant:  $d_{max} = 0.7$ ,  $\alpha = 10$ ,  $\beta = 0.5$ ).

The model world in which our virtual species expands is one-dimensional, has closed boundaries, and is made of discrete patches in which individuals live and between which they may disperse. Patches, which form the spatial units of the model, are characterized by their location  $x$  (integer  $\geq 0$ ), by their current population size  $N$ , and by their carrying capacity  $K$ , the latter being equal and constant among all patches.

Individuals each possess three dispersal traits, a maximal dispersal rate  $d_{max}$ , a relative slope  $\alpha$ , and a midpoint  $\beta$ . Each individual dispersal probability then depends on these traits and local population density  $N$  at the start of the dispersal phase (**Fig. 1**, Kun and Scheuring 2006). Following the terminology in Cote et al (2017), variation in  $d_{max}$  can be interpreted as encoding variation in dispersal enhancing or enabling traits, while variation in  $\alpha$  or  $\beta$  corresponds to variation in dispersal matching traits. We allow  $\beta$  to be negative instead of being constrained to be always  $\geq 0$ , as this is the most convenient way to generate flat dispersal-density functions that preserve the ecological meaning of  $d_{max}$  (see detailed discussion in **Supplementary Materials S1 and S2**). To allow for genetic and non-genetic variation, each trait is actually encoded as the (transformed) sum of an underlying additive genetic component and an underlying noise/residual part; i.e.  $d_{max} = \text{logit}^{-1}(a_{[d_{max}]} + r_{[d_{max}]})$ ,  $\alpha = a_{[\alpha]} + r_{[\alpha]}$ ,  $\beta = a_{[\beta]} + r_{[\beta]}$ , where  $a$  and  $r$  denote the additive genetic and residual components respectively. To track neutral genetic diversity, individuals also possess a neutral locus  $\gamma$  at which two allelic values are possible (0 or 1).

Once we know the  $d_{max}$ ,  $\alpha$  and  $\beta$  of an individual, we additionally calculate three values at the individual level:  $d_0$ , the hypothetical dispersal rate at  $N = 0$ ;  $d_K$ , the expected dispersal rate at  $N = K$ ; and the difference between  $d_K$  and  $d_0$   $\Delta_{K-0} = d_K - d_0$ , which we use as our measure of the strength of dispersal density-dependence.

The model is initialised by releasing  $K$  adult individuals that have not yet dispersed nor reproduced in the patch  $x = 0$ . Initial values for the genetic and non-genetic components of individual traits  $a$  and  $r$  are drawn from Normal distributions, with the value of initial heritability  $h^2$  used to determine how initial phenotypic variance is partitioned between genetic and non-genetic components (see **Virtual experiment design** and **Fig. 2** below for the values of initial means and variances in this study). Initial allelic values for the neutral locus are drawn from Bernoulli(0.5). The world is set to be long enough that the expansion never runs out of patches. As dispersers can only move by one patch (see below) and the expansion advances in one direction, this means, in practice, that the world can be any number of patches as long as it is larger than the number of generations in a run (for run duration in our experiment, see **Virtual experiment design**).

Generations are non-overlapping, and every time step, the life cycle unfolds as follows:

- Individuals are counted, providing information about patch population sizes  $N$  for dispersal;
- *Dispersal*: Newly adult individuals may disperse with a probability  $d$  depending on their individual traits ( $d_{max}$ ,  $\alpha$ ,  $\beta$ ) and local population size  $N$ :  $d = \frac{d_{max}}{1 + \exp\left(-\alpha\left(\frac{N}{K} - \beta\right)\right)}$  (**Fig. 1**, Kun and Scheuring 2006). Individuals that do disperse die with a probability  $m$ ; if they survive, they settle in one of the immediate neighbouring patches, randomly chosen.
- Individuals are re-counted post-dispersal, updating population sizes  $N$  for the reproduction phase;
- *Reproduction*: Each remaining adult then produces  $F$  juveniles, with  $F \sim \text{Poisson}(\lambda)$  and the mean fecundity  $\lambda$  based on a Ricker model:  $\lambda = e^{r_0(1-N/K)}$ , where  $r_0$  is the low-density growth rate. Juveniles are born in the patch currently occupied by their parent, and directly inherit their genetic values for dispersal-

related and neutral loci. Their values for the noise part of the dispersal traits are redrawn at random.

- *Death and end of cycle*: All adults die; juveniles then become adults.

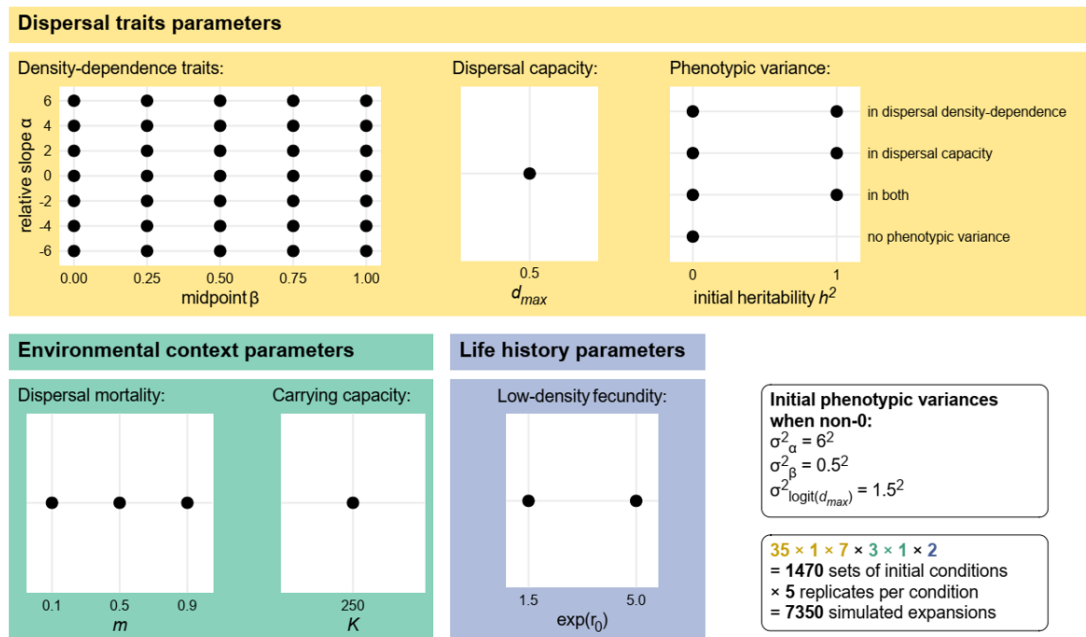
To facilitate further analyses, a series of patch-level summaries of traits are computed by the model every generation. In this study, we are particularly interested in the patch-level means of  $d_{max}$ ,  $d_0$  and the density-dependence metric  $\Delta_{K-0}$ , as well as in the neutral allele frequencies (all collected right before the dispersal phase).

### *Simulation experiments and analyses*

#### *Virtual experiment design*

We simulated all possible combinations of the starting parameters described in **Fig. 2**, and replicated each of the resulting 1470 combinations (hereafter "scenarios") five times, for a total of 7350 replicates. We ran simulations for 120 generations (in practice 121, so that metrics collected pre-dispersal were still collected after 120 generations of expansion). Preliminary explorations show that most expansions in our individual-based model reach a stable linear speed within 25 to 50 generations. The low-density growth rate  $r_0$  was constant within a given replicate, with two possible values chosen to be compatible with existing data from a range of arthropods in experimental contexts (e.g. Bowler and Benton 2009; Wagner et al. 2017; Szűcs et al. 2017b; Vercken et al. 2021). The chosen  $K$  is within an order of magnitude of typical population sizes seen during experimental range expansions in plants or invertebrates (e.g. Ochocki and Miller 2017; Van Petegem et al. 2018; Williams and Levine 2018; Dahirel et al. 2021). The non-zero value for the initial phenotypic variance of  $\text{logit}(d_{max})$  (**Fig. 2**) was chosen because a  $\text{Normal}(\mu = 0, \sigma = 1.5)$  distribution on the logit scale leads to an approximately uniform distribution over most of the  $[0; 1]$  range on the proportion scale (e.g. McElreath 2020). The range of starting values for the initial mean of  $\alpha$  was chosen based on a key property of the logistic function used to model dispersal:  $d$  goes from  $0.05 \times d_{max}$  to  $0.95 \times d_{max}$  over an interval of width  $\simeq 6/|\alpha|$  centered on  $\beta$  (e.g. Börger and Fryxell 2012). Setting the initial  $|\alpha|$  to be 6 means that interval is of width  $\simeq K$ . The initial phenotypic variance for  $\alpha$  was then set so that the difference between the minimal (-6) and maximal (6) initial  $\alpha$  was 2

standard deviations. A similar argument was used to set the initial phenotypic variance for the midpoint  $\beta$ .



**Figure 2.** Summary of the global parameters used in our model, and the initial values used in our simulation experiments.

## Analyses

Simulation outputs were analysed using R, version 4.3.1 (R Core Team 2023). Simulated data handling and plotting relied primarily on the `tidyverse` suite of packages (Wickham et al. 2019), as well as the `patchwork` (Pedersen 2020) and `ggtext` packages (Wilke and Wiernik 2022). In all our main analyses, we only used data about the initial conditions and the state of the expansions at the end of the simulations ( $t = 121$ , but effectively after 120 generations of expansion since traits are collected prior to the dispersal phase). Unless noted, in the analyses that required statistical modelling, we used the `brms` package (Bürkner 2017) as a convenient front-end for the Bayesian language Stan (Carpenter et al. 2017), along with the `bayesplot` (Gabry et al. 2019) and `tidybayes` (Kay 2019) packages for checking and handling posteriors and predictions. We used "weakly informative" priors largely based on McElreath (2020): `Normal(0,1.5)` for intercepts interpretable as the logit of a proportion, `Normal(0,1)` for all other fixed effects, and `Half – Normal(0,1)` for random effects standard deviations. All models



showed satisfactory convergence, effective sample sizes and posterior predictive checks (Gabry et al. 2019; Vehtari et al. 2021). All code to reproduce the analyses described below is archived and publicly available (**Data availability**).

### Expansion velocity

In theory, the velocity of a pulled expansion can be predicted directly from the low-density dispersal and growth rates alone (e.g. Lewis et al. 2016; Gandhi et al. 2016; Birzu et al. 2019; Wang et al. 2019). Positive density-dependence in dispersal should lead to higher speeds than expected from these predictions, and the ratio between the actual expansion velocity  $v$  and the velocity  $v^*$  calculated from low-density traits only is the primary marker of whether an expansion is pushed (Birzu et al. 2018, 2019; Gandhi et al. 2019). However, in our context, there are several elements that make it difficult to use directly this  $v/v^*$  ratio in statistical models: first, dispersal mortality, by decreasing the effective growth and dispersal rates can bring  $v$ ,  $v^*$  or both to 0; second, because velocities are bounded between 0 and 1 in our simulations, the ratio  $v/v^*$  can be artificially reduced if there are velocities in the vicinity of either boundary. Therefore, we instead used a simpler qualitative and graphical approach. We first estimated  $v^*$  using the relevant discrete space/ discrete time equations in Wang et al. (2019), in which we used the net dispersal rates and per-capita fecundities after accounting for losses due to dispersal mortality. We then plotted observed velocities (using the distance between the starting patch and the farthest populated patch after 120 generations of expansions, divided by time) against their corresponding  $v^*$ , and examined how expansions of varying density-dependence  $\Delta_{K-0}$  fell relative to the  $y = x$  line. We also displayed the line resulting from the least-squares linear regression of  $v$  on  $v^*$  for the subset of replicates with  $\Delta_{K-0} = 0$ ; this line is expected to fall slightly lower than the  $y = x$  line due to the effect of demographic stochasticity (Brunet et al. 2006; Hallatschek and Korolev 2009; Gandhi et al. 2016). We plotted separately the scenarios with no phenotypic variation in dispersal ( $N = 1050$ ), the scenarios with phenotypic variation in at least one trait but no genetic variation ( $N = 3150$ ), and the scenarios where trait evolution is possible ( $N = 3150$ ).

## Genetic diversity

In a system with one biallelic neutral locus as in this study, drift should eventually lead one of the alleles to fixation at the expansion edge, while the other lags behind (Roques et al. 2012). Dividing the expansion into a "lagging" and a "leading" fraction based on which neutral allele individuals possess, we can use the ratio between the expansion speeds of the lagging fraction relative to the speed of the whole expansion as our measure of genetic diversity retention in space during expansion (hereafter "genetic diversity" or "genetic diversity retention"), with pushed expansions expected to have larger values. As the denominator (expansion time) is the same for both fractions, this simplifies to a ratio of counts of colonised patches that can be statistically analysed using (Beta-)Binomial models. As the fate of genetic diversity during expansion is dependent on an actual expansion happening, replicates that either went fully extinct or failed to advance beyond the starting patch ( $N = 109$ ) were excluded, resulting in a total set of 7241 replicates. We note that extinctions and failures to advance are not randomly distributed across replicates: they all occur in expansions with high dispersal mortality and low fecundity, and almost all in expansions with no evolution (**Supplementary Material S3**). Even though, due to the way  $d_0$  and  $\Delta_{K-0}$  are correlated in our experimental design, these failures all occur in replicates with negative  $\Delta_{K-0}$ , the range of initial  $\Delta_{K-0}$  available in actually expanding expansions remains the same in these high mortality / low fecundity contexts than in the overall dataset (**Supplementary Material S3**).

On that set, we ran three separate Beta-Binomial generalized linear mixed models (Harrison 2015) with the data split as for the velocity data above: one model for the scenarios with no phenotypic variation ( $N = 1012$ ), one for the scenarios with phenotypic variation in at least one trait but no genetic variation ( $N = 3084$ ), and one for all the scenarios where trait evolution is possible ( $N = 3145$ ). In all three cases, fixed effects included initial density-dependence  $\Delta_{K-0}$  at  $t = 0$ , dispersal mortality (as a three-level factor), fecundity (as a two-level factor) and all two-way and three-way interactions. We additionally included "scenario" as a random intercept that accounts for differences between scenarios that are not explained by these fixed effects (because  $\Delta_{K-0}$  does not capture all the variation in the shape of the dispersal-density curve generated by variation in  $\alpha$  and  $\beta$ ). We used Beta-Binomial models because posterior checks on initial Binomial

models showed evidence of overdispersion, and we allowed the overdispersion parameter  $\phi$  to vary between scenarios in the same way as the mean (same fixed and random effect variables), as further checks showed that such models performed much better than models with a unique  $\phi$ .

#### Evolution of dispersal at the expansion front

In this study, we are interested in how traits evolve at the range front, i.e. the area at and close to the edge of the expansion where recently-founded populations have not yet reached an equilibrium density. This means we first need to define which patches belong to the range front. Based on plots showing the distribution of population sizes as a function of distance to the farthest-forward population (**Supplementary Material S4**), we decided the 5 patches closest from the edge of the expansion (including the edge patch itself) belong to the range front for the purposes of analyzing phenotypic trait dynamics (note that this also matches choices in Erm and Phillips 2020). Patches closer to the core typically have already reached an equilibrium density (which may or may not be  $K$ , depending on the interplay between growth and dispersal; **Supplementary Material S4**). For each replicate expansion, we used weighted averages (based on population size at the time of trait measurement) to average trait values across front patches before analyses. After 120 generations, the genetic variance in  $\alpha$ ,  $\beta$  or  $\text{logit}(d_{max})$  in these front patches is consistently close to 0 in the expansions where these traits can evolve (**Supplementary Material S5**), indicating that traits should have (mostly) finished evolving.

As our measure of density-dependence  $\Delta_{K-0}$  is a difference between high and low-density dispersal, its range of possible values is constrained by the maximal dispersal rate  $d_{max}$  and may expand or contract, even if the distributions of  $\alpha$  and  $\beta$  remain stable, if  $d_{max}$  increases or decreases (see how the difference between  $d_0$  and  $d_K$  varies between curves in **Fig. 1A**). To better separate changes in  $d_{max}$  from those in matching traits, we therefore analyse on one hand the *relative* density-dependence  $\Delta_{K-0}/d_{max}$ , and then on the other hand  $d_{max}$  itself.

We first used a Beta generalized linear mixed model (Douma and Weedon 2019) to analyse how relative density-dependence  $\Delta_{K-0}/d_{max}$  (rescaled from [-1,1] to [0,1] for model fitting) after expansion varied between replicates. We only used the subset of non-

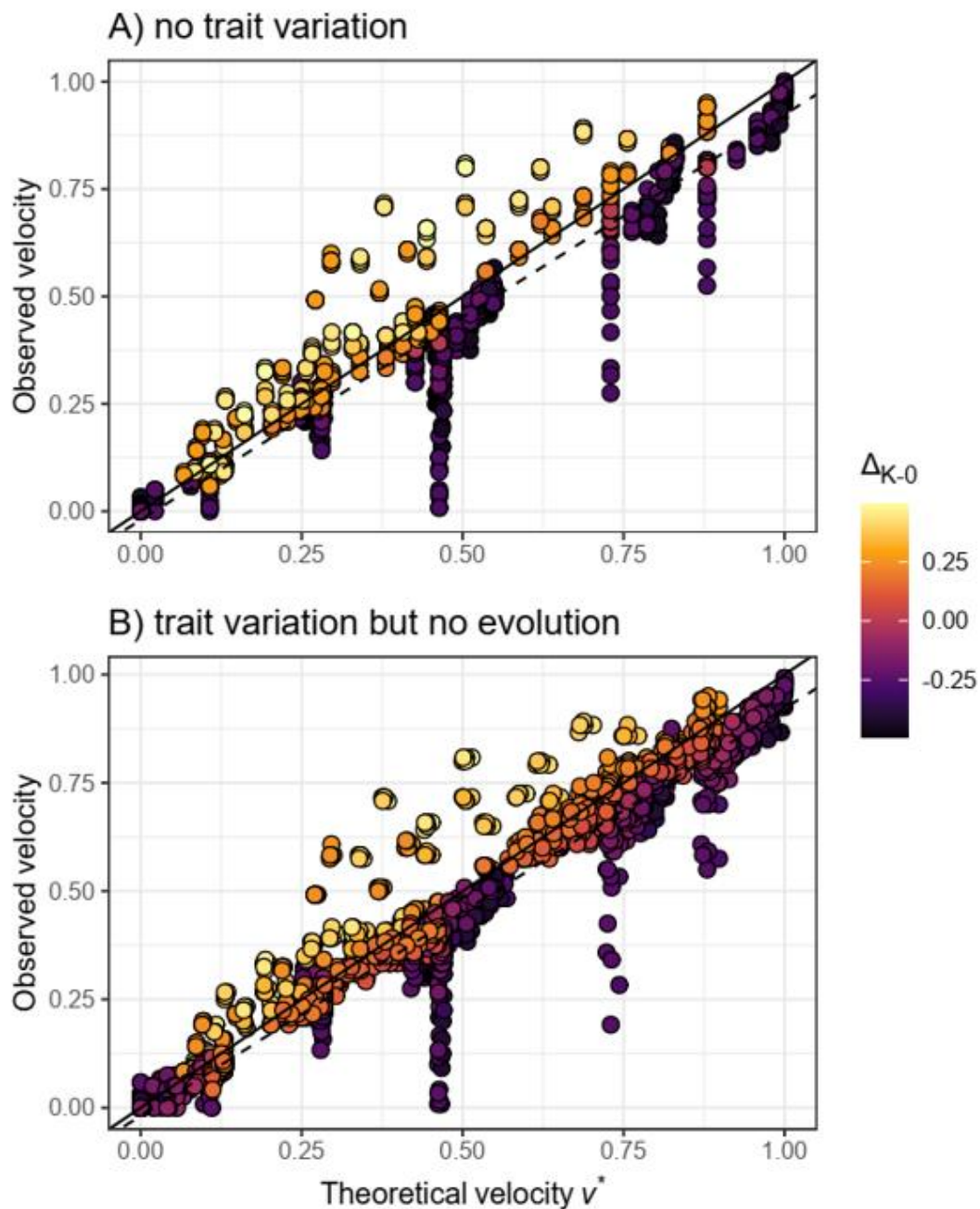
extinct and expanding replicates with heritable variation in  $\alpha$  and  $\beta$  ( $N = 2098$ ), since by definition those are the only expansions in which  $\Delta_{K-0}/d_{max}$  can evolve at the front. We then used another Beta generalized mixed model to analyse how the mean maximum dispersal rate  $d_{max}$  after expansion varied between replicates. Here we used the subset of non-extinct and expanding replicates that had initial heritable variation in  $\text{logit}(d_{max})$  ( $N = 2096$ ). Both models included the same fixed and random effect structure as genetic diversity models: fixed effects of initial  $\Delta_{K-0}$  before expansion, fecundity, dispersal mortality and all two- and three-way interactions, as well as scenario random intercepts, both for the mean and for the overdispersion parameter  $\phi$ . Initial density-dependence was included as  $\Delta_{K-0}$ , rather than  $\Delta_{K-0}/d_{max}$ , for consistency with the genetic diversity models; this has no bearing on the results since the initial mean  $d_{max}$  is virtually identical across all replicates (with minor variations only due to random sampling of initial trait values).

## Results

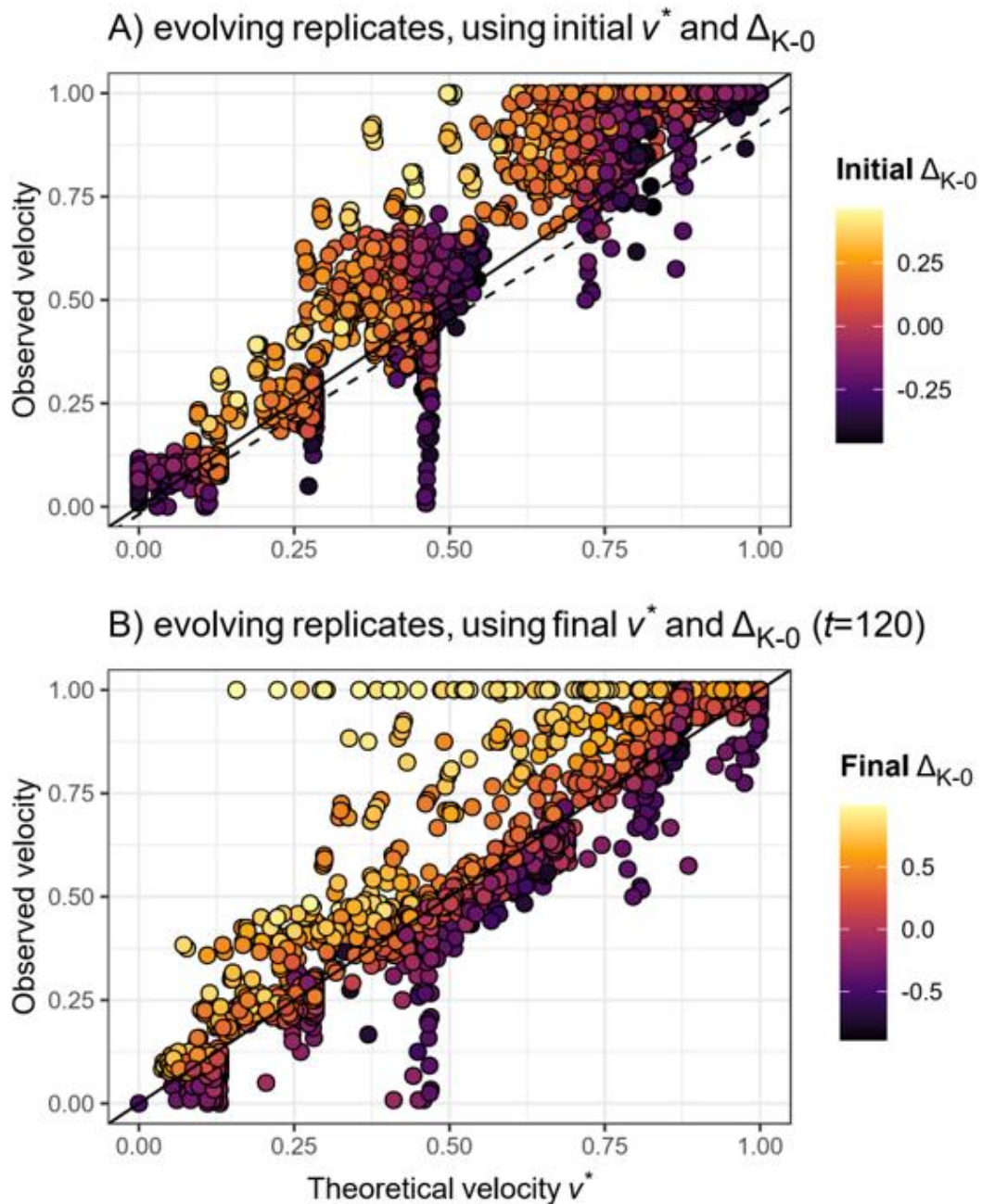
### *Expansion velocity*

In the absence of trait variation, the theoretical velocity  $v^*$  is a very good predictor of observed expansions velocities (Fig. 3A,  $r = 0.94$ ). Nevertheless, expansions where dispersal increased with density ( $\Delta_{K-0} > 0$ ) were often faster than  $v^*$ , while expansions where dispersal decreased with density were often slower (Fig. 3A). The results are similar if non-genetic trait variation is added (Fig. 3B,  $r = 0.97$ ). When traits are allowed to evolve, the dynamics are more complex. While  $v^*$  remains a very good predictor of observed velocities ( $r = 0.95$  for both panels of Fig. 4), the relationship between  $\Delta_{K-0}$  and "excess" speed depends strongly on whether  $\Delta_{K-0}$  and  $v^*$  are calculated based on initial dispersal trait values or trait values at the front at the end of simulations. If the former, expansions tend to be faster than expected based on  $v^*$  at high  $v^*$ , irrespective of dispersal density-dependence (Fig. 4A). If the latter, we recover the qualitative patterns described in the absence of evolution, with expansions where  $\Delta_{K-0} > 0$  faster than  $v^*$  and expansions where  $\Delta_{K-0} < 0$  slower (Fig. 4B), albeit with many more expansions reaching the maximal velocity of 1. For a breakdown of the evolutionary data between expansions where the

maximum dispersal rate can evolve and those where it could not, which does not change meaningfully the qualitative descriptions above, see Supplementary Material S6.



**Figure 3.** Relationship between observed expansion velocities and expected theoretical velocities  $v^*$ , in the absence of trait evolution. Each replicate is coloured according to its value of dispersal density-dependence. The full straight lines correspond to  $y = x$ , the dotted line are linear regressions for the replicates with  $\Delta_{K-0} = 0$  only; the slight mismatch between the two lines is expected from theory (see **Methods**).

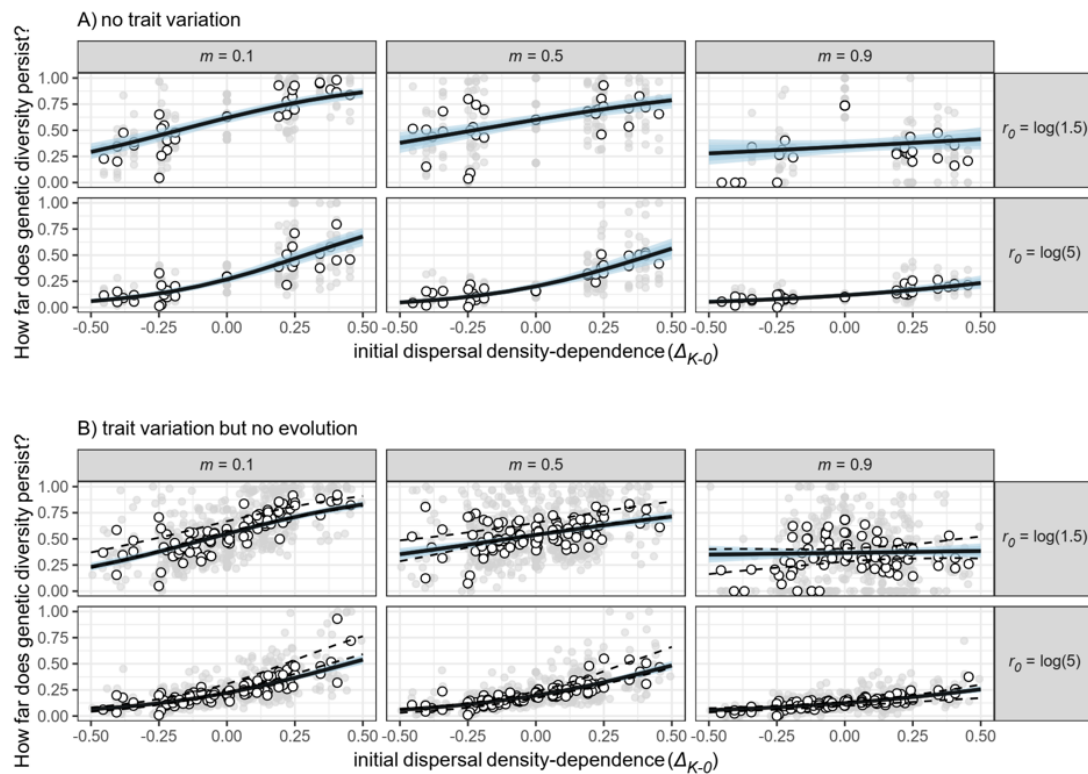


**Figure 4.** Relationship between observed expansion velocities and expected theoretical velocities  $v^*$ , in expansions where traits could evolve. In (A),  $v^*$  and dispersal density-dependence  $\Delta_{K-0}$  are both calculated based on the initial distribution of dispersal traits, as in **Fig. 3**; in (B) they are instead calculated based on traits at the range front after evolution, at the end of the simulated expansion. Each replicate is coloured according to its value of dispersal density-dependence (note the different scales in (A) and (B)). The full straight lines correspond to  $y = x$ , the dotted line in (A) is the linear regression from **Fig. 3B**, i.e. for the replicates with  $\Delta_{K-0} = 0$  only in the absence of evolution.

*Genetic diversity*

In the absence of trait variation, genetic diversity retention increased with dispersal density-dependence  $\Delta_{K-0}$  when dispersal mortality was low or intermediate ( $m = 0.1$  or  $0.5$ ) (**Fig. 5A**; left and middle columns). However, when dispersal mortality was high ( $m = 0.9$ ), genetic diversity retention at the end of the simulations was overall lower, and the effect of dispersal density-dependence was weaker (**Fig.5A**; right column). Indeed, the effect of mortality was mostly concentrated on expansions with positive density-dependent dispersal: their genetic diversity decreased with increased mortality much more than other expansions (**Fig. 5A**). These effects were consistent across both levels of fecundity, although at lower fecundity high dispersal mortality canceled, rather than simply reduced, the effect of density-dependence (**Fig.5A**; bottom row vs. top row). In addition, expansions with higher fecundity had a consistently lower ability to retain genetic diversity.

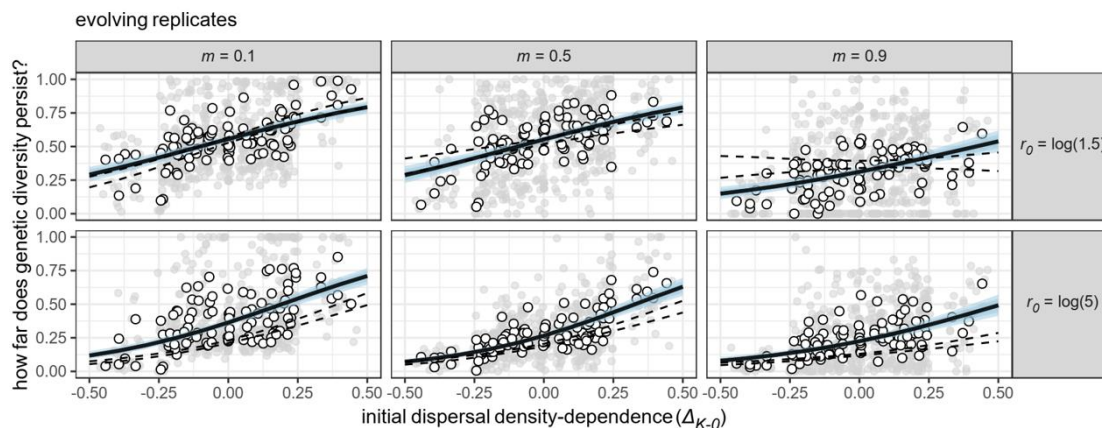
Results in the presence of fully non-genetic trait variation were qualitatively and quantitatively very similar (**Fig. 5B**), to the point differences might be attributable simply to more precise estimates due to a larger number of replicates.



**Figure 5.** Effect of initial dispersal density-dependence on the maintenance of neutral genetic diversity across expansions, in the absence of evolution. Grey dots are observed values per replicates, white dots the average values per scenario (as defined **Fig. 2**), and the full line + blue band are the predictions and 95% credible intervals from the corresponding statistical model. In (B) the dashed lines are the 95% credible intervals from (A), overlaid for comparison.

Allowing dispersal traits to evolve had two main consequences on the relationship between *initial*  $\Delta_{K-0}$  and genetic diversity retention (**Fig. 6**). First, when fecundity is high, evolving replicates maintain genetic diversity farther into the expansion than their equivalent non evolving replicates. Second, allowing dispersal to evolve restored the positive relationship between density-dependence and diversity in replicates with high mortality, when it was absent (at low fecundity) or dampened (at high fecundity) in non-evolving replicates. Interestingly, this positive relationship between  $\Delta_{K-0}$  and genetic diversity was restored differently depending on fecundity: by increasing the expected diversity at high  $\Delta_{K-0}$  when fecundity is high, but by both increasing the expected diversity at high  $\Delta_{K-0}$  and decreasing it at low  $\Delta_{K-0}$  when fecundity is low (**Fig. 6**).

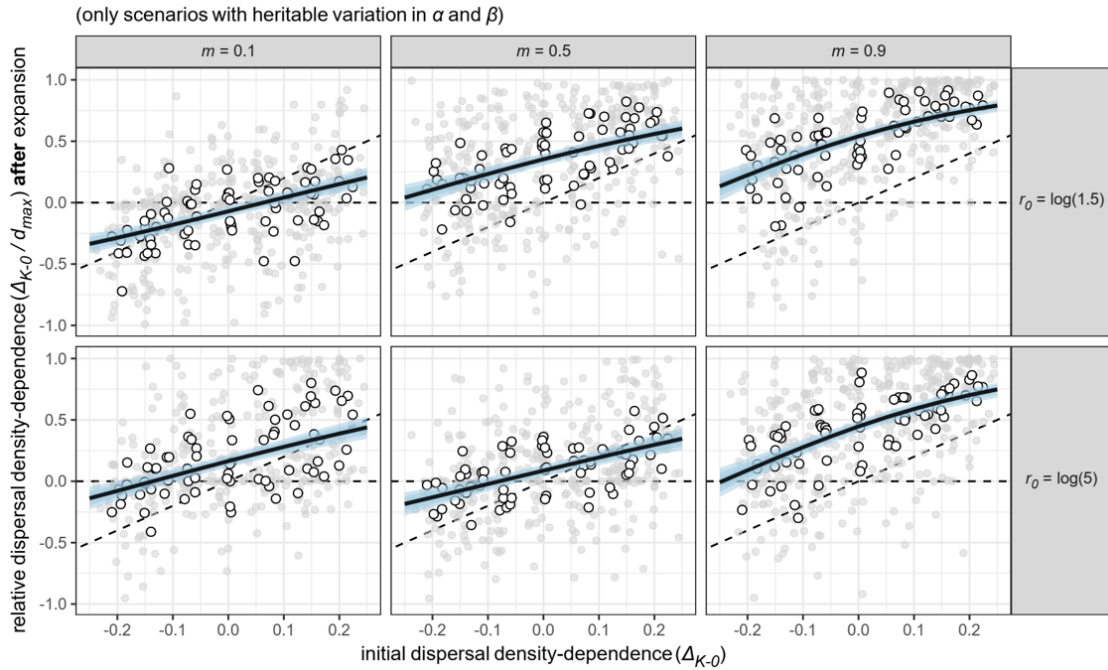




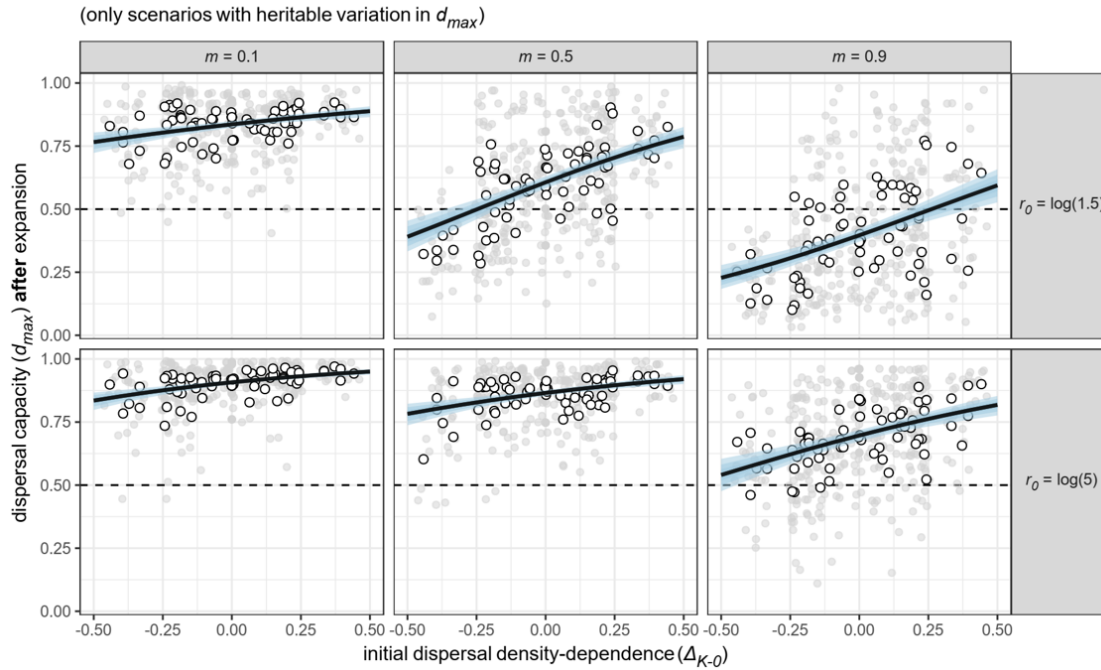
**Figure 6.** Effect of initial dispersal density-dependence on the maintenance of neutral genetic diversity across expansions, when at least one trait is allowed to evolve. Grey dots are observed values per replicates, white dots the average values per scenario (as defined **Fig. 2**), and the full line + blue band are the predictions and 95% credible intervals from the corresponding statistical model. The dashed lines are the 95% credible intervals from **Fig. 5B** (similar initial phenotypic variation but no evolution), overlaid for comparison.

#### *Evolution of dispersal phenotypic traits*

Dispersal trait evolution is strongly dependent on initial dispersal density-dependence  $\Delta_{K-0}$ : across all dispersal mortality or fecundity values, replicates with initial  $\Delta_{K-0} > 0$  consistently evolve higher values of both  $\Delta_{K-0}/d_{max}$  and  $d_{max}$  at the expansion front compared to replicates with initial  $\Delta_{K-0} < 0$  (**Figs 7, 8**). However, the actual direction of evolution (towards overall increases or decreases) does vary depending on mortality and fecundity. Overall, expansions become more positively density-dependent after evolution ( $\Delta_{K-0}/d_{max}$  increases) across most contexts (**Fig. 7**). A major exception is when both dispersal costs and fecundity are low: in these cases, expansions that started with  $\Delta_{K-0}/d_{max} > 0$  do evolve towards lower values at the front (**Fig. 7**, top left). A few individual scenarios also present this pattern in other contexts, especially with  $m < 0.9$  (**Fig. 7**), but not enough to shift the average predictions. When dispersal costs are low,  $d_{max}$  consistently evolves to higher values at the range front (**Fig. 8**). Higher dispersal costs or lower fecundity reduces the post-evolution values of  $d_{max}$ , to the point  $d_{max}$  can evolve to end up below its 0.5 starting value if costs are high, fecundity is low, and expansions started with negative dispersal density-dependence (**Fig. 8**, top right).



**Figure 7.** Effect of initial dispersal density-dependence ( $\Delta_{K-0}$ ) on *relative* dispersal density-dependence  $\Delta_{K-0}/d_{max}$  at the expansion front after evolution. Grey dots are observed values per replicates, white dots the average values per scenario (as defined **Fig. 2**), and the full line + blue band are the predictions and 95% credible intervals from the corresponding statistical model. The diagonal dashed lines correspond to the absence of evolution (initial  $d_{max}$  is 0.5 in all replicates); the horizontal dashed lines mark the limit between positive and negative density-dependence of dispersal after evolution.



**Figure 8.** Effect of initial dispersal density-dependence ( $\Delta_{K-0}$ ) on the maximal dispersal rate  $d_{max}$  at the expansion front after evolution. Grey dots are observed values per replicates, white dots the average values per scenario (as defined **Fig. 2**), and the full line + blue band are the predictions and 95% credible intervals from the corresponding statistical model. The horizontal dashed lines correspond to the absence of evolution.

## Discussion

A large number of experimental and observational studies have described how dispersal is often density-dependent, across a wide range of taxa (reviewed in Matthysen 2005; Harman et al. 2020), and many models have been developed to understand under what conditions density-dependent vs density-independent dispersal evolves and is maintained, in both expanding and non-expanding ranges (e.g. Travis et al. 1999; Travis et al. 2009; Rodrigues and Johnstone 2014; Baines et al. 2020; Deshpande and Fronhofer 2023). Until recently (Erm and Phillips 2020), studies of pushed vs. pulled expansions have almost entirely ignored the implications of trait evolution. Even then, that study was focused on pushed expansions created by Allee effects only, meaning we do not know how dispersal evolution shapes whether an expansion stays or become pushed or pulled. We here used a series of individual-based simulations as a first attempt to address this

gap. We first confirmed that our measure of dispersal density-dependence was a good metric of expansion "pushiness", as in the absence of evolution, we recovered classical results on the link between positive density-dependence and (i) excess velocity relative to predictions for pulled expansions (**Fig. 3**; (e.g. Lewis et al. 2016; Birzu et al. 2019; Zhu et al. 2023)), (ii) genetic diversity (**Fig. 5**, see below for a detailed discussion). This is despite our density-dependence metric being very simplistic, merely a difference between dispersal at low density vs. at carrying capacity. This is promising for the application of theoretical insights to real world contexts, as it means that one does not need to collect detailed information about the shape of the dispersal-density relationship to obtain relevant results. We then examined in more detail the consequences of dispersal evolution on genetic diversity and on dispersal density-dependence itself.

#### *Dispersal costs and evolution shape the relationship between density-dependence and genetic diversity*

We find that in the absence of dispersal variation, neutral genetic diversity in our simulations generally behaves as expected from theory (Roques et al. 2012; Birzu et al. 2018, 2019), with some nuances however that may be key for its applicability in more general or ecologically realistic contexts. As predicted, neutral genetic diversity loss was slowed down when dispersal was positively density-dependent (**Fig. 5**), a key property of pushed expansions (Roques et al. 2012; Birzu et al. 2019). However, this was only true when dispersal costs were low or moderate. At high costs of dispersal, this relationship was strongly dampened, or even cancelled out entirely at low fecundities (**Fig. 5**). We cannot fully exclude that the latter is in part a reflection of the non-random distribution of extinct or non-expanding replicates, which were concentrated in scenarios with no evolution, low fecundity, high mortality and  $\Delta_{K-0} < 0$  (**Supplementary Material S3**). First however, we note that this non-random extinction pattern does not actually shrink the range of density-dependence values in that part of the data (**Supplementary Material S3**). Second, we note that it is actually not only the link between density-dependence and diversity that vanishes in expansions with low fecundity and high mortality: the expected relationship between density-dependence and expansion velocity seemingly does too (see **Supplementary Material S7** for a focus on these expansions, which are the ones with the lowest  $v^*$  **Fig. 3**). In any case, similar analyses in "real world" contexts (*in natura* or in

lab experiments) would also likely be focused on successful expansions only for the same reasons; our general point remains therefore valid. Our results here establish that dispersal costs can create plausible scenarios where the positive relationship between density-dependence and genetic diversity, which has been seen as a canonical property of pushed expansions (Birzu et al. 2019), may actually vanish. Increased costs of dispersal are known to lead to lower genetic diversity during expansions (e.g. Mona et al. 2014). While dispersal density-dependence may compensate for this, it may be that the net effect is still negative if dispersal costs are too high. Importantly though, we find that allowing dispersal traits to evolve can actually restore the expected relationship between density-dependence and diversity even at high mortality and low fecundity (**Fig. 6**). We suggest that dispersal evolution at the range front (see discussion below) is a key mechanism behind this effect: scenarios that evolved stronger positive density-dependence by either increasing relative density-dependence or  $d_{max}$  have higher diversity than their non-evolving counterparts, while scenarios that evolved lower values of either trait do not, or even have lower diversity (compare **Fig. 6** with **Figs 7, 8**).

Our results here highlight once again the importance of dispersal costs in shaping the dynamics of spatially distributed populations (Bonte et al. 2012), and show that pushed expansion models that do not account for these costs may overgeneralize. This might make their predictions potentially less useful in contexts where these costs become non-negligible, which may be common given how ubiquitous fragmented habitats are at the global scale, especially due to human impacts (e.g. Ibisch et al. 2016).

*Costs of dispersal and fecundity determine when dispersal evolution leads pushed expansions to become more pulled*

Our simulations show that the strength and direction of evolution at the range edge is to some extent predictable, if we have information about both environmental characteristics (dispersal costs) and initial trait values (**Figs. 7, 8**). For instance, although the maximum dispersal rate  $d_{max}$  generally evolved towards higher values at the front due to spatial sorting, this was dependent on both dispersal costs and initial density-dependence (see below). There still remains substantial amounts of unexplained variation however (see the spread of individual replicates **Figs. 7, 8**). This is in line with previous work showing that

evolutionary stochasticity and serial founder events can lead to high variability in evolutionary outcomes and spread dynamics between initially identical or near-identical expansions (Phillips 2015; Weiss-Lehman et al. 2017; Dallas et al. 2020). As already discussed by these authors and others, this puts an intrinsic limit on our ability to predict the evolutionary trajectories and spread of *single* range expansions before they start; this includes here whether they will stay or become pushed/pulled.

We find that Erm and Phillips (2020)'s key prediction, that pushed expansions tend to become pulled with time, is only fulfilled under a narrow set of conditions in our model where it is dispersal, not growth, that is allowed to increase with density. Simulated expansions starting from pushed dynamics (positive dispersal-density slope) only moved consistently towards more pulled dynamics when both mortality *and* fecundity were low (**Fig. 7**), although low dispersal costs alone were enough to move some scenarios towards pulled expansions. When these conditions were not fulfilled, pushed expansions tended to stay pushed, and pulled expansions either stayed pulled or actually became pushed with time (**Fig. 7**).

The interplay between fecundity levels and the evolution of density-dependence has precedents in the literature (e.g. Travis et al. 1999); although the outcome may differ, both because of the different dispersal-density models (simple increasing line vs increasing or decreasing sigmoid function) and the different context (non-expanding vs expanding), the same general principles likely apply here. For a given carrying capacity  $K$  and if dispersal costs are small enough, the fitness benefit obtained by moving from crowded patches close to  $K$  to less crowded (or even empty) habitats is higher if individuals have high fecundity than if they have low fecundities. This may mean that when dispersal costs are small, low-fecundity individuals will disperse more independently of density and at lower levels than high fecundity individuals, as in our results (**Figs. 7, 8**).

Our results showing that dispersal tends to stay positively density-dependent are in line with existing dispersal theory, which predicts that higher costs of dispersal favour positive density-dependent dispersal strategies (Travis et al. 1999; Rodrigues and Johnstone 2014). On the other hand, they seemingly contrast with insights from Travis et al. (2009), which did model range expansions contrary to the above two studies, and showed that dispersal

tended to become more consistently high independently of densities. However, there may not be any contradiction here: upon closer examination, Travis et al. (2009) do suggest that evolution towards density-independent dispersal during expansions is stronger at the range edge when costs of dispersal are low, which again matches our results. On the empirical side, our simulations also reproduce qualitatively results from a previous experimental study involving two of the authors (Dahirel et al. 2021). The microwasp *Trichogramma brassicae* started range expansions with positive density-dependent dispersal and would thus demonstrate pushed dynamics in the absence of evolution. However, individuals at the edge rapidly evolved to develop more negative density-dependence, but only when connectivity was high (and thus presumably costs were low). The fact that under some other contexts, evolution can lead to more, not less, positive density dependence in dispersal at range edges, is also supported experimentally by at least one study (Mishra, Chakraborty, et Dey 2020).

Allowing the maximum dispersal rate  $d_{max}$  to evolve may actually limit even more the possibilities of dispersal evolution towards more pulled expansions. Indeed and as expected (e.g. Travis et al. 2009),  $d_{max}$  tended to increase at the range front, unless dispersal costs were very high (**Fig. 8**). If relative dispersal density-dependence ( $\Delta_{K-0}/d_{max}$ ) is held constant, increasing  $d_{max}$  will increase the magnitude of the absolute density-dependence  $\Delta_{K-0}$ , and it is that absolute dependence that drives whether an expansion is pushed (Wang et al. 2019). In other terms, if an expansion is already pushed, evolution of higher dispersal alone may make it more pushed, even if the traits linked to density-dependence itself do not evolve. Importantly for our consideration of pushed expansion evolution, expansions that started pushed tended to evolve higher  $d_{max}$  than those that did not (**Fig. 8**), strengthening this effect even more. This contradicts hypotheses put forward by Birzu et al. (2019), that evolutionary changes in dispersal motility would not influence "pushiness", because they assumed these changes would affect dispersal quantitatively the same way across the range of densities, contrary to what can happens using Kun and Scheuring (2006)'s dispersal model. This shows that the way dispersal is modelled may play a critical role in our expectations of its consequences (see also Deshpande and Fronhofer 2023), and that models that distinguish between

dispersal capacity and context-dependence traits (Cote et al. 2017) may behave differently from those that do not.

*Towards more realistic representations of phenotypic variation?*

Overall, and although further exploration of the parameter space is needed, our results suggest that pushed expansions caused by density-dependent dispersal may be "resistant" to evolutionary transformation into pulled expansions under many circumstances. Given how common positive density-dependent dispersal is (Harman et al. 2020), this has clear implications for our ability to predict or understand evolutionary dynamics in range expansions. Furthermore, we show that the fate of pushed vs. pulled expansions under dispersal evolution depends both on the environmental context and on which dispersal traits can evolve. To forecast if a given expansion will likely stay pushed, with the associated implications in terms of velocity or genetic diversity, we may therefore need better information about the degree of genetic variation in not only dispersal capacity, but also dispersal reaction norms (Saastamoinen et al. 2018), information that is currently lacking for many species, including expanding ones.

While our model is arguably more complex than many models of pushed expansions, especially due to the addition of evolution, it still makes some key simplifications, which may need to be reexamined in the future to determine how they influence our conclusions.

First, we used asexual haploid virtual organisms and each dispersal trait was shaped by one locus only; evolutionary dynamics might be influenced by the reproductive system, or the number of loci involved in inheritance and their genetic architecture (Saastamoinen et al. 2018; Deshpande and Fronhofer 2023). Some simulations suggest that while these may influence the strength of evolutionary change during expansion (and its effect on expansion velocity), they might not change the overall direction of the evolutionary response (Weiss-Lehman and Shaw 2021). These results remain however to be confirmed in the context of pushed expansions. We also ignored mutation for simplicity and focused only on the fate of initial standing variation at introduction, rather than long-term mutation-selection equilibria. Work by Erm and Phillips (2020) suggests that adding



mutation would merely accelerate/accentuate trait differentiation compared to what we observed, as it would provide variation allowing spatial sorting to continue.

Second and most critically, we only studied the effect of dispersal evolution. Whether or not an expansion is pushed, and to what degree, depends on both dispersal and population growth (Birzu et al. 2019; Zhu et al. 2023), and the latter can be further subdivided in its fundamental life history components, fecundity and survival. The present study already shows how the outcome of dispersal evolution and its consequences for diversity can depend on baseline fecundity, even in the absence of any trade-offs or individual variation in life history. However, fecundity and survival can actually vary among individuals, and can also be density-dependent, potentially in ways that could cancel each other and dispersal out (for examples of such cancellation in a non-evolutionary context, see Zhu et al. 2023). They may also be correlated in syndromes at the within- and/or among-species level (Guerra 2011; Ronce and Clobert 2012; Beckman et al. 2018; Jacob et al. 2019; Ochocki et al. 2020), and these syndromes may shape and constrain the evolution of their constituent traits (Ronce and Clobert 2012; Wright et al. 2019), including during range expansions (Ochocki et al. 2020; Urquhart and Williams 2021). In addition, theoretical work even suggests that density fluctuations themselves are one of the root evolutionary drivers shaping the (co)variation of life history traits, and potentially their association with behaviours such as dispersal (Wright et al. 2019, 2020). How the complexities of phenotypic structure and trait coevolution drive the net effect of population density on spread, influencing the dynamics of pushed or pulled expansions and our ability to predict them, remain to be explored.

## Data availability

Netlogo model code and R scripts to reproduce all analyses presented in this manuscript are available on Github (<https://github.com/mdahirel/pushed-pulled-2020-heritability-IBM>) and archived in Zenodo (<https://doi.org/10.5281/zenodo.5830993>). Simulation outputs are also archived in Zenodo (<https://doi.org/10.5281/zenodo.5830996>).

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## Author contributions

Funding: EV; initial manuscript idea: MD and EV; simulation model development: MD and CG; simulated data analysis: MD; initial manuscript draft: MD. All authors read and edited the manuscript, and approved the final version.

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## Supplementary Material for "Individual variation in dispersal shapes the fate of pushed vs. pulled range expansions"

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### S1 - Detailed description of the individual-based model in the ODD format

#### *Purpose and patterns*

The model simulates asexual individuals reproducing and dispersing in a linear landscape following an initial introduction, in order to approximate processes at play during natural and experimental range expansions. The aim is to gather insights into how evolutionary dynamics (neutral diversity and dispersal-related traits) and expansion velocity are shaped by trait distribution (means and variances) at the start of the expansion. We specifically focus on traits driving the position of expansions on the pushed/pulled continuum (Birzu et al., 2018, 2019), namely traits shaping the density-dispersal function. Importantly, dispersal and reproduction are stochastic. The focus of the model is on studying the effects of initial trait variation at introduction; as such there is no mutation, for simplicity.

#### *Entities, state variables and scales*

Individuals are haploid and reproduce asexually, and can vary in:

- their location in the landscape ( $x$  coordinate only, since we simulate linear landscapes.  $x$  can only take  $\geq 0$  integer values);
- their dispersal probability  $d$  (real between 0 and 1) and the underlying dispersal traits ( $d_{max}, \alpha, \beta$ ). Each trait is the (transformed) sum of an additive genetic component ( $a_{[d_{max}]}, a_{[\alpha]}, a_{[\beta]}$ ) and of a noise/residual part ( $r_{[d_{max}]}, r_{[\alpha]}, r_{[\beta]}$ ). All these components are reals. See **Initialization** and **Submodels** below for details about the dispersal function;
- the allelic value at a neutral locus  $\gamma$  (binary, 0 or 1);

- their life stage (juvenile or adult, coded as a binary variable);
- their fecundity  $F$  ( $\geq 0$  integer).

We note that the model as it is coded and made available (see **Data availability** in main text) is more general and allows the use of diploid, sexually reproducing individuals, with some slight adaptations in the reproduction submodel. For simplicity we only use and describe the "haploid asexual" scenario here.

Individuals live in discrete patches, which form the spatial units of our model. The model world is one-dimensional, and has closed boundaries. Patches can be described by:

- their location in the landscape ( $x$  coordinate;  $\geq 0$  integer values);
- their population size at the last count  $N$  ( $\geq 0$  integer; population counts occur at points of the cycle where only adults are present);
- their carrying capacity  $K$  ( $\geq 0$  integer;  $K$  is fixed and constant across all patches);
- a series of variables summarizing the trait distributions of the individuals born in the patch (see **Submodels**).

One time step in the model represents one generation of the simulated species' life cycle, and each individual grid cell corresponds to an individual patch. The potentially hostile matrix between patches is abstracted out (there are no "matrix" grid cells) and its effects are summarised in a global environmental variable, dispersal mortality  $m$ . The spatial and temporal extents of the simulations are not fixed and can be set up based on the needs of the simulation experiments.

#### *Process overview and scheduling*

Generations start at the point of the life cycle where only pre-dispersal, pre-reproduction adults are present. The schedule of a generation can be divided in 6 processes: *initial Population count*, *Summary statistics*, *Dispersal*, *second Population count*, *Reproduction*, and *Death*. All individuals and patches must go through one process before the model proceeds to the next. The order in which individuals/patches go through a given process is random.

- *Population count*: Individuals at each patch are counted to update the patch population sizes  $N$  and the neutral allele frequencies for each patch.

- *Summary statistics*: Patches estimate a series of summary variables describing the trait distribution of individuals they currently harbour. This is done because exporting and analyzing individual-level traits would be computationally expensive. A list of the summary variables is provided in **Submodels** below.
- *Dispersal*: Adult individuals may disperse with a probability  $d$  depending on their individual traits  $(d_{max}, \alpha, \beta)$  and local population size  $N$  **at the start of the dispersal phase**. The dispersal model is taken from Kun and Scheuring (2006) and described in **Submodels** below. If an individual attempts to disperse, it dies during the attempt with a probability  $m$ . As the model is coded in base Netlogo, which does not include the possibility to directly from Bernoulli or Binomial distributions, a workaround is used. In practice we draw random values from a Uniform(0, 1) distribution; if the draw is lower than  $d$  (respectively  $m$ ), the individual disperses (respectively dies). Surviving dispersers are randomly moved to one of the nearest neighbouring patches; that is, the maximal dispersal distance is of 1 patch.
- *Second population count*: The population sizes  $N$  and neutral alleles frequencies at each patch are updated again.
- *Reproduction*: Each remaining adult then produces  $F$  juveniles, with  $F$  drawn from a Poisson distribution and depending on the general growth rate  $r_0$ ,  $K$  and  $N$ . Juveniles are born in the patch currently occupied by their parent (same  $x$ ), and also inherit their genetic values for dispersal-related and neutral loci. Their values for the noise part of the dispersal traits are redrawn at random. The exact fecundity model and inheritance procedures are described in **Submodels** below.
- *Death and end of cycle*: All adults die; juveniles then become adults.

The model then starts the next generation. We chose to make dispersal precede reproduction, so that our model simulates *natal dispersal*, i.e. the movement from birth site to the first reproduction site, arguably the most studied and best understood type of dispersal.

### *Design concepts*

**Basic principles**: This model follows previous attempts to model evolution in range expansions using an individual-based simulation framework (e.g. Travis et al., 2009), including in the context of pushed expansions (e.g. Erm & Phillips, 2020). This model is a

theoretical investigation tool and is not built to make any real-world quantitative prediction, but to develop new qualitative insights about evolutionary dynamics during range expansions. It differentiates itself from previous modelling studies of pushed expansions in an ecological/evolutionary context by:

- the use of a more flexible dispersal function (Kun & Scheuring, 2006).
- a focus on "small" population sizes that are realistic for many "macroscopic" organisms, giving a more important role to discreteness, drift and stochasticity in general, compared to models assuming much larger population sizes either implicitly (e.g. when using continuum models) or explicitly (Birzu et al., 2019).
- the possibility of varying trait heritability, where most models either ignore evolutionary dynamics in focal traits (e.g. Birzu et al., 2019) or assume all variation is genetic (e.g. Erm & Phillips, 2020).

**Emergence:** The number and distribution of individuals and alleles in space are the emergent result of individual dispersal and reproduction, which are stochastic and themselves depend, recursively, on the distribution of individuals in space. Most if not all variables of interest are summaries from these distributions.

**Adaptation:** As population size varies in space and time along the range expansion, dispersal is costly, and fitness is density-dependent (see **Submodels**), dispersal can evolve in an adaptive way in replicates where dispersal traits are heritable.

**Objectives:** There is no direct objective-seeking in this model, in the sense that individuals do not adjust their dispersal behaviour *for* increasing their expected fitness. However, the model allows for evolution; in these cases, natural selection based on differential reproductive success may lead lineages to maximize their reproductive success through time.

**Learning:** Individuals do not learn (see **Sensing**).

**Prediction:** There is no prediction component to individuals' choices: individuals behave only based on currently available information, including their phenotype.

**Sensing:** In addition to its own trait values, the only information an individual can sense and use is the (last updated) population size  $N$  in the patch it is currently in. Individuals automatically and accurately know  $N$  when needed, and immediately forget it afterwards (there is no memory).

**Interaction:** Individuals do not interact directly with each other. Individuals in the same patch may influence each other indirectly, through the patch population size variable  $N$  which plays a role in both individual dispersal and reproduction.

**Stochasticity:** Dispersal and reproduction are both stochastic. First, for dispersal, the individual probability of dispersing depends on three traits, the values of which are determined stochastically. The genetic components are drawn from Normal distributions at the start of the experiments (and then transmitted deterministically), and the noise components are drawn from Normal distributions at the birth of every individual. Second, once the individual dispersal probability is set, whether or not an individual actually disperses, and whether or not it dies if it disperses, is in effect determined by Bernoulli trials (implemented by determining if a (pseudo-)random number between 0 and 1 is higher or lower than the relevant probability). Finally, the actual fecundity of each individual is a random draw from the relevant Poisson distribution. See **Initialization** and **Submodels** for more details.

**Collectives:** Individuals do not belong to any kind of identifiable social group or collective *per se*. Individuals in the same discrete patch nonetheless influence each other through  $N$  (see **Interaction**)

**Observation:** For memory reasons, it is impractical to save the state of every individual. We instead measure and record patch-level metrics, which convey information about population size, neutral allele frequencies and the means and variances of variables summarizing the dispersal-density functions of individuals born in the patch (see **Submodels**). The user can choose to save these metrics every generation, or for only a subset of generations of interest.

### Initialization

Each expansion starts by creating the landscape (which, as we use nearest-neighbour dispersal, can be any length higher than the number of generations planned for the run), and setting the carrying capacity of all patches to  $K$ . We then introduce  $K$  adult individuals that have not yet dispersed or reproduced to the left-most patch of the landscape ( $x = 0$ ). All other patches are empty. Individual traits and alleles are then initialized as follows:

- the value (0 or 1) at the neutral allele  $\gamma$  is drawn from Bernoulli(0.5) (in practice implemented by randomly selecting an integer between 0 or 1).
- for each dispersal trait  $z$  (logit( $d_{max}$ ),  $\alpha$ ,  $\beta$ ), the genetic component is drawn from Normal ( $\bar{z}_{t=0}$ ,  $\sqrt{h^2 V_{P[z]}}$ ), the noise component from Normal(0,  $\sqrt{(1 - h^2) V_{P[z]}}$ ), where  $\bar{z}_{t=0}$  is the initial mean trait value,  $h^2$  is the initial trait heritability and  $V_{P[z]}$  the initial phenotypic variance. The trait value is then obtained by summing the genetic and noise components, and in the case of  $d_{max}$ , back-transforming the sum from the logit scale:  $d_{max} = \text{logit}^{-1}(a_{[d_{max}]} + r_{[d_{max}]})$ ,  $\alpha = a_{[\alpha]} + r_{[\alpha]}$ ,  $\beta = a_{[\beta]} + r_{[\beta]}$ .
- we calculate secondary individual-level statistics from  $d_{max}$ ,  $\alpha$  and  $\beta$  (see the Dispersal submodel description below).

### Input data

The model is self-sufficient and does not use external input data to represent time-varying processes.

### Submodels

**Dispersal:** during the dispersal phase, an individual leaves its natal patch with a probability  $d$ , which depends on individual traits and local population size  $N$  as measured at the start of the dispersal phase (here expressed relative to the constant  $K$ ) based on Kun and Scheuring (2006)'s model (see also Travis et al., 2009):

$$d_N = \frac{d_{max}}{1 + \exp(-\alpha(\frac{N}{K} - \beta))}.$$

Compared to other dispersal models (such as those reviewed in Hovestadt et al., 2010), this three-parameter model has the advantage of flexibility, can model a wide variety of realistic dispersal curves, and allows for both negative and positive density-dependent dispersal. In addition, all three parameters have an ecologically relevant interpretation:

- $d_{max}$  is the maximal dispersal rate, and can be seen as a measure of dispersal capacity. Note that depending on the other parameters,  $d_{max}$  may not be reachable at any of the population sizes actually experienced during the simulation.
- $\alpha$  is the slope of the dispersal-density relationship and describes the "strength" of the response to population density (relative to  $d_{max}$ ). Whether  $\alpha$  is positive or negative determines whether dispersal increases or decreases with population size. Depending on  $\beta$ ,  $\alpha$  may or may not influence meaningfully the actual dispersal strategy at the population sizes experienced during the simulation.
- $\beta$  is the inflection point of the dispersal function, i.e. the density at which  $d = 0.5 \times d_{max}$ . It can be interpreted as a response threshold, i.e. how high (or low) density must get for the individual to substantially alter its dispersal response. We allow  $\beta$  to be negative; this can be interpreted as individuals being so sensitive to density that they already are close to their high density dispersal behaviour at low densities. For our purpose, this is the only practical way the model can produce density-independent functions where  $d \approx d_{max}$  (as setting  $\alpha$  to 0 actually sets  $d$  to be constant, but  $= 0.5 \times d_{max}$ ). Another way is theoretically possible: allowing  $\beta$  to be close to 0 or  $K$  but positive, and  $|\alpha|$  to be so high (for a given  $K$ ) that dispersal goes from 0 to  $d_{max}$ , or the opposite, between  $N = 0$  and  $N = 1$  (as in e.g. Travis et al., 2009). However, due to how  $\alpha$  influences the shape of the dispersal function, Normal distributions of initial  $\alpha$  that allow for such high  $|\alpha|$  would be strongly biased against shallower slopes (see **Supplementary Material S2**).

Following the terminology in Cote et al (2017), variation in  $d_{max}$  can be interpreted as encoding variation in dispersal enhancing or enabling traits, while variation in  $\alpha$  or  $\beta$  corresponds to variation in dispersal matching traits.

Once we know the  $d_{max}$ ,  $\alpha$  and  $\beta$  of an individual, we additionally calculate three values at the individual-level:

- $d_0$ , the hypothetical dispersal rate at  $N = 0$ . The theoretical distinction between pulled and pushed expansions hinges on whether expansion move as fast as expected from  $d_0$  or faster (e.g. Birzu et al., 2019).
- $d_K$ , the expected dispersal rate at  $N = K$ .
- A measure of the strength of density-dependence  $\Delta_{K-0} = d_K - d_0$ .

We note that the model can easily be modified to add instructions for other metrics describing additional aspects of the shape of the density-dispersal function.

**Reproduction:** Each adult individual still living during the reproduction stage produces  $F$  offspring, with  $F \sim \text{Poisson}(\lambda)$  and the average offspring number  $\lambda$  depending on local population size  $N$  based on a Ricker model:

$$\lambda_N = e^{r_N}, r_N = r_0 \left(1 - \frac{N}{K}\right),$$

where  $r_0$  is the hypothetical *per capita* growth rate at  $N = 0$ .

Parent transmit their genetic values (dispersal-related:  $a_{[d_{max}]}$ ,  $a_{[\alpha]}$ ,  $a_{[\beta]}$  and neutral:  $\gamma$ ) directly to their offspring without any mutation. Offspring then draw random values of noise components  $r_{[d_{max}]}$ ,  $r_{[\alpha]}$ ,  $r_{[\beta]}$  from  $\text{Normal}(0, \sqrt{h^2 V_{R[z]}})$ , where  $z$  is the trait in question. For each trait  $z$ , the "random noise" variance  $V_R$  is equal to  $(1 - h^2)V_{P[z]}$ , where  $h^2$  is the *initial* heritability at  $t = 0$  and  $V_P$  the *initial* phenotypic variance.

Observation:

The code estimates and reports a variety of summary variables at the patch level, typically means and variances of individual-level traits, as well as counts of individuals, and can easily be modified to add more. Of potential interest are the following:

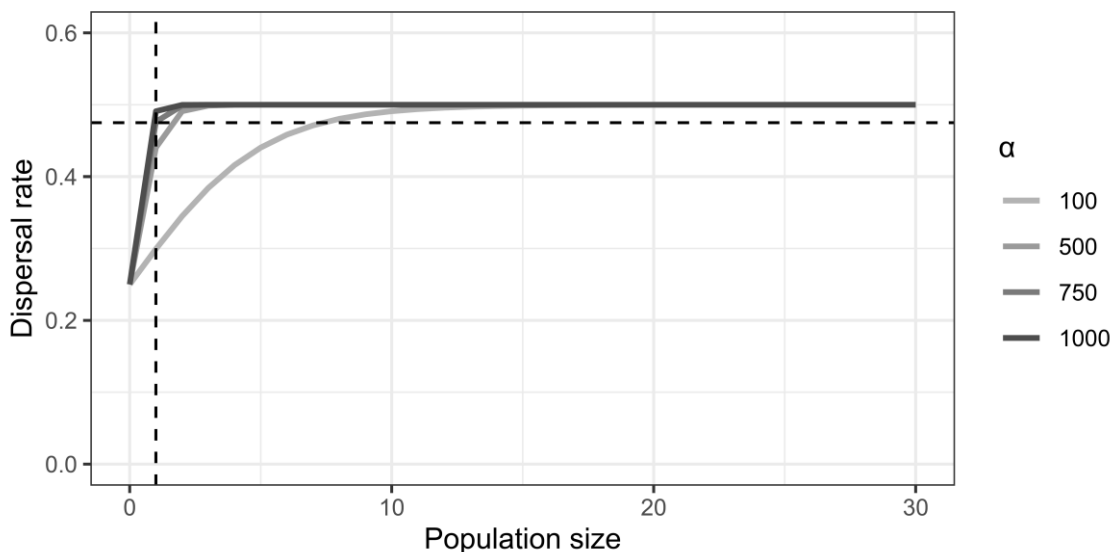
- the means of  $d_{max}$ ,  $d_0$ ,  $\Delta_{K-0}$  for all individuals born in a patch.
- the variances of the genetic components  $a_{[d_{max}]}$ ,  $a_{[\alpha]}$ ,  $a_{[\beta]}$  for all individuals born in a patch.
- population sizes  $N$  pre- and post-dispersal phase.
- the frequencies of the two neutral alleles in a patch, both pre- and post-dispersal phase.



## S2 - Effect of the magnitude of initial variation in $\alpha$ on density dependence

In the ODD description above, we briefly discuss how allowing for negative  $\beta$  is the only way we have to create mostly flat dispersal-density function where dispersal is close to  $d_{max}$ . We briefly explain that one seeming alternative, forcing  $\beta$  to stay  $\geq 0$  and allowing very large  $|\alpha|$  values so that dispersal goes from 0 to close to  $d_{max}$  between  $N = 0$  and  $N = 1$ , is not viable for our purposes. We expand this argument here.

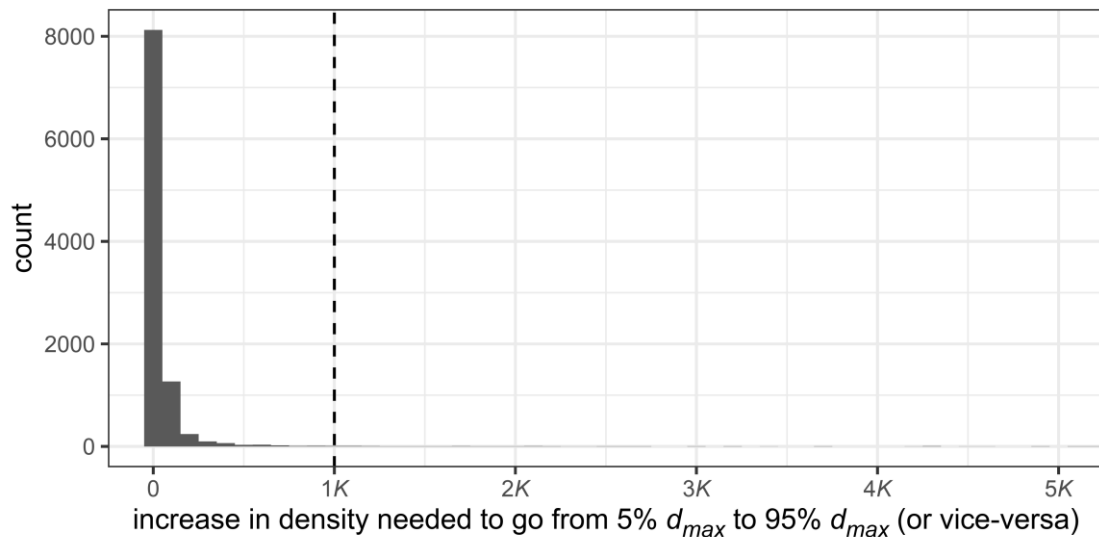
Using very large  $\alpha$  means we'd need the initial trait distribution to contain both these very large  $\alpha$  (positive and/or negative) *and*  $\alpha$  close to 0, for evolution to be possible (in the absence of mutation at least). It's easy to demonstrate that distributions that fulfill this requirement are actually biased towards very sharp density-dispersal functions. If we assume  $K = 250$  as in our simulations, then  $\alpha$  close to 1000 are needed to generate one of these nearly flat functions (**Fig. S2.1**):



**Figure S2.1.** Example of how one can produce a functionally flat density-dispersal function using a very sharp slope  $\alpha$  ( $d_{max} = 0.5$ ,  $\beta = 0$ ). The dashed lines mark  $N = 1$  (vertical) and  $d_N = 0.95 \times d_{max}$  (horizontal).

So, even after setting  $\beta$  at 0, we still need  $\alpha$  in the neighbourhood of 1000 to be able to produce such shapes (when, as a reminder,  $\alpha = 6$  is needed to get a slope that takes a population increase of  $K$  individuals to go from 5% to 95% of  $d_{max}$ , so a reasonably shallow, but not too shallow function). An initial distribution of  $\alpha$  of Normal(0, 500) would

hit these extreme  $\alpha$  with low but non-negligible probabilities. And we know (see main text) that  $6/\alpha$  approximately expresses (in units of  $K$ ) how sharp the increase in dispersal with density is. Let's have a look at the distribution of  $6/|\alpha|$  implied by  $\alpha \sim \text{Normal}(0, 500)$  (**Fig. S2.2**):



**Figure S2.2.** Distribution of the increases in density needed to go from 5% of  $d_{max}$  to 95%, assuming  $\alpha \sim \text{Normal}(0, 500)$ . Histogram drawn based on 10000 samples, the  $x$  axis is cut at 5K for better visualisation.

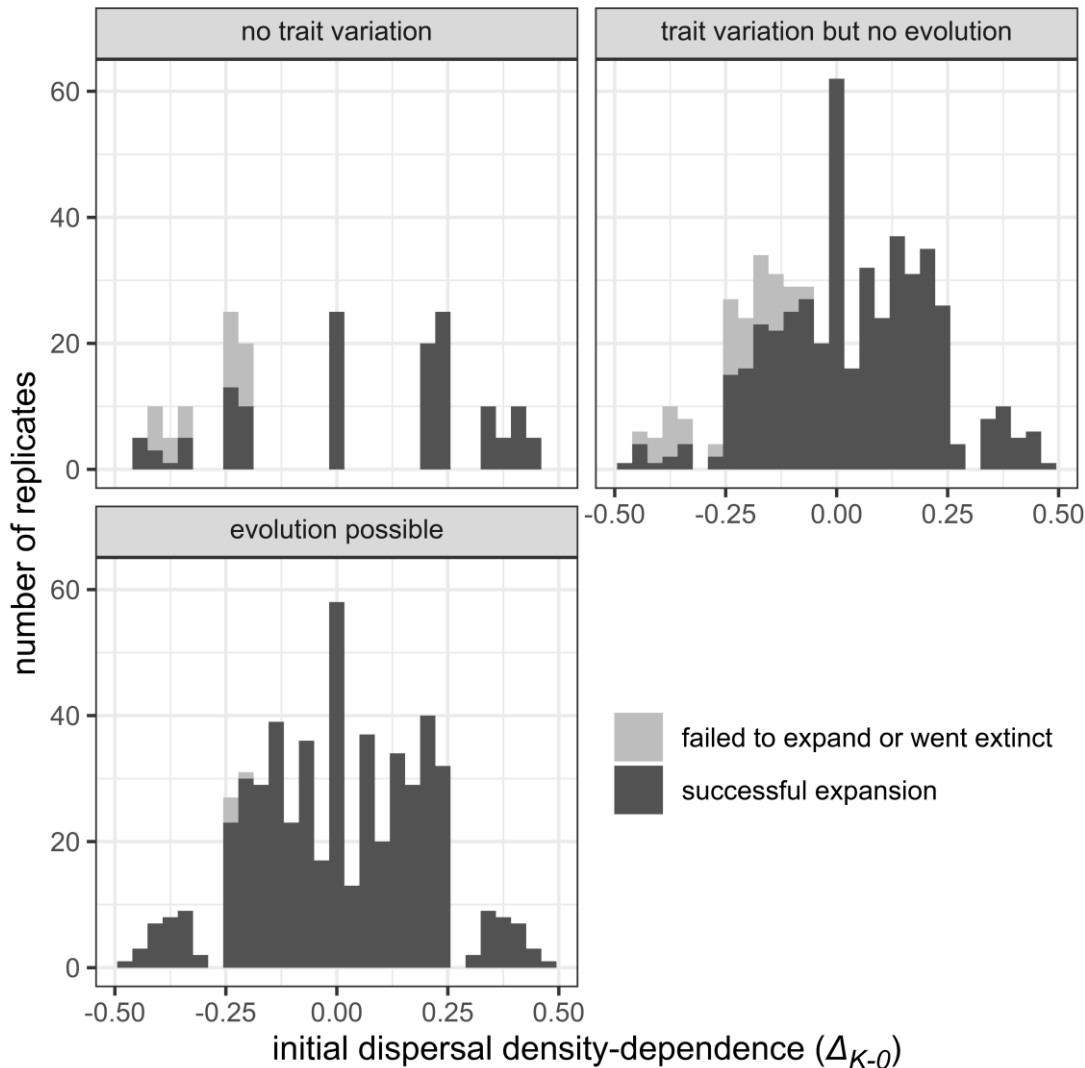
We can see that this initial distribution of  $\alpha$  would mostly only allow sharp slopes, that take less than 20-50% $K$  to go from (nearly) 0 to (nearly)  $d_{max}$ , and shallower slopes would only be present at much lower frequencies. This is not a choice that is ecologically sound in our opinion; hence why we rejected "extreme  $\alpha$ " as a method to generate  $d_N \approx d_{max}$  flat functions.

### S3 - Distribution of the replicates that failed to expand

Exploring data shows that all 109 replicates that either went extinct or otherwise failed to expand had low fecundity ( $r_0 = \log(1.5)$ ) and high dispersal mortality ( $m = 0.9$ ). Looking into this subset of the data in more detail (**Fig. S3.1**), we find that:

- most failed expansions are in replicates where evolution is not allowed. This suggests a role of evolutionary rescue;

- failed expansions all have negative initial density-dependence  $\Delta_{K-0}$ ;
- however, this does not reduce the available range of density-dependence for analyses that rely on only successful expansions, and most replicates with  $\Delta_{K-0} < 0$  successfully expand.

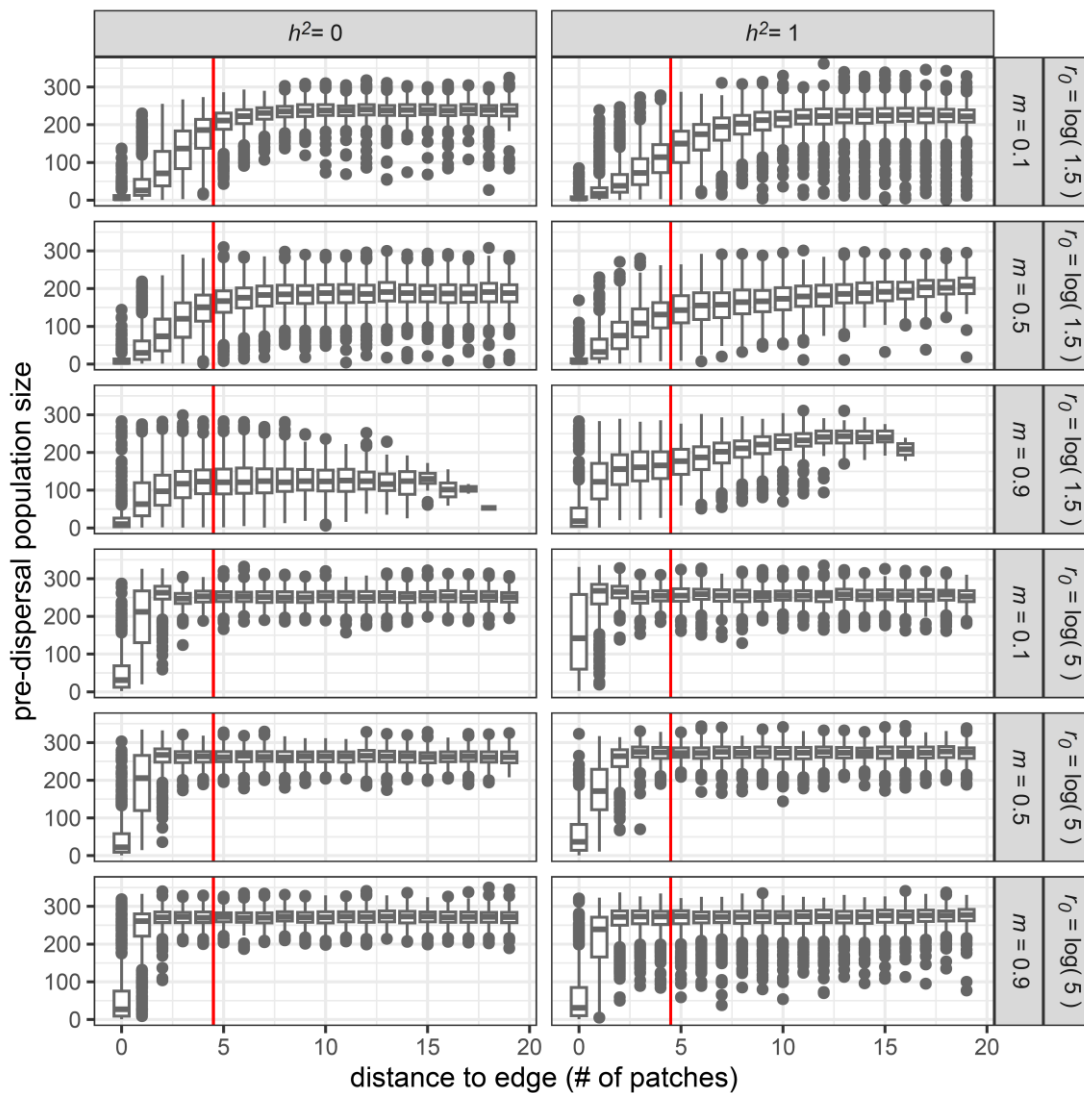


**Figure S3.1.** Distribution of the simulation replicates based on their initial density-dependence  $\Delta_{K-0}$  and on whether they successfully expanded by  $t = 120$  or went extinct/remained stuck at  $x = 0$ . Only replicates with low fecundity ( $r_0 = \log(1.5)$ ) and high dispersal mortality ( $m = 0.9$ ) are displayed, since expansions under other conditions were all successful.

## S4 - How do we define the "range front"?

We are interested in how traits at the front of the expansion are shaped by, and shape, the expansion process. To do that right, we need an operational definition of what is the front. A "traditional" one is the range of patches where a density gradient is seen, i.e.

where population density has not yet reached its equilibrium (e.g. Gandhi et al., 2016; Lewis et al., 2016).



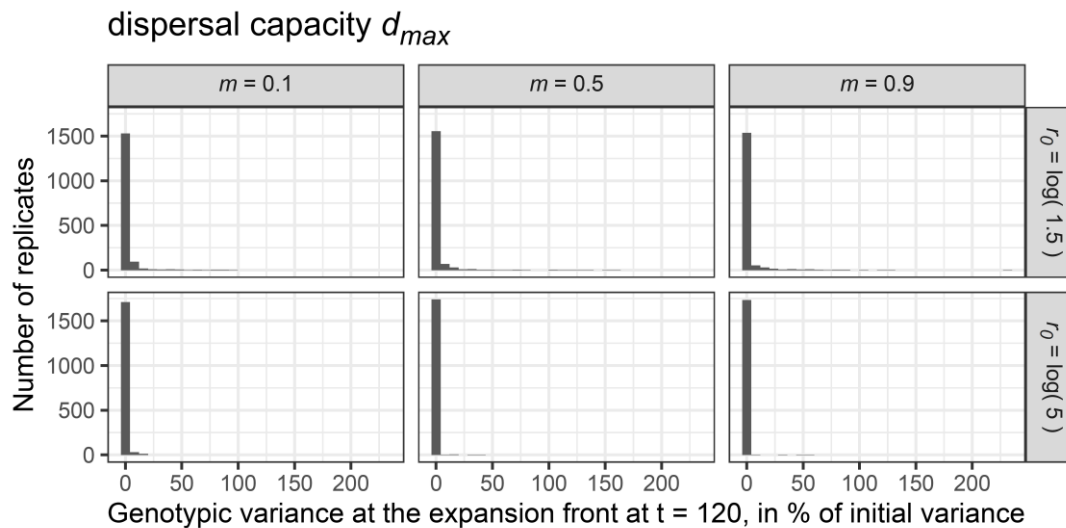
**Figure S4.1.** Predispersal population size as a function of distance to the range edge (only populations up to 20 patches from the edge at the time of sampling included). The vertical line separate the 5 patches closest from the edge from the others.

We can see **Fig. S4.1** that a threshold where we consider the 5 patches closest from the edge (edge patch included) as belonging to the range front is a good compromise that works across conditions. Narrower fronts would probably work for the high fecundity scenarios, but would not work for the low fecundity ones. In addition, a narrower threshold would limit the number of individuals included, reducing the precision of our trait means, while a

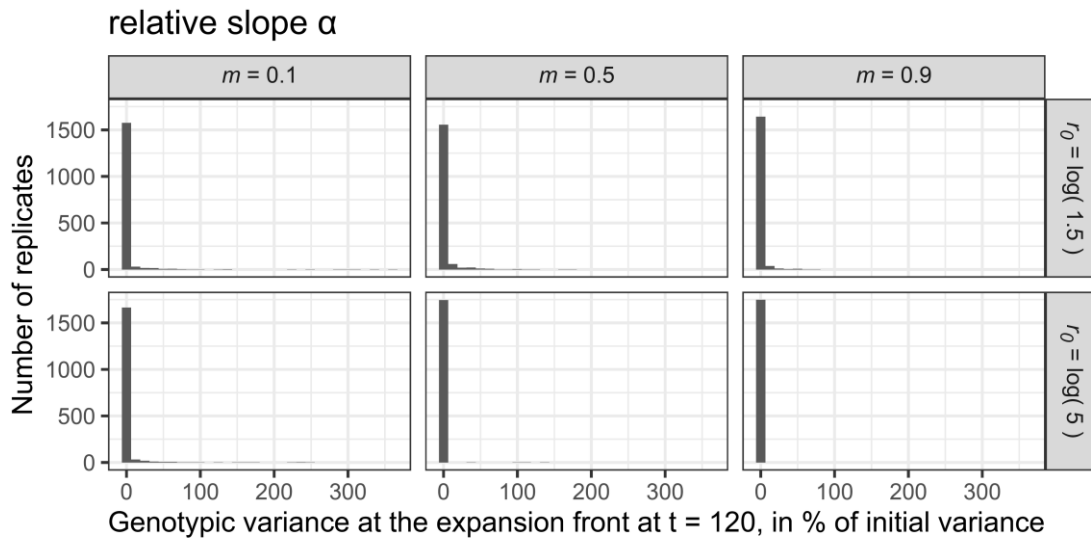
wider one would lead us to fronts that are dominated by what are clearly non-front patches when fecundity is high.

## S5 - Genetic variation at the end of the simulated expansions

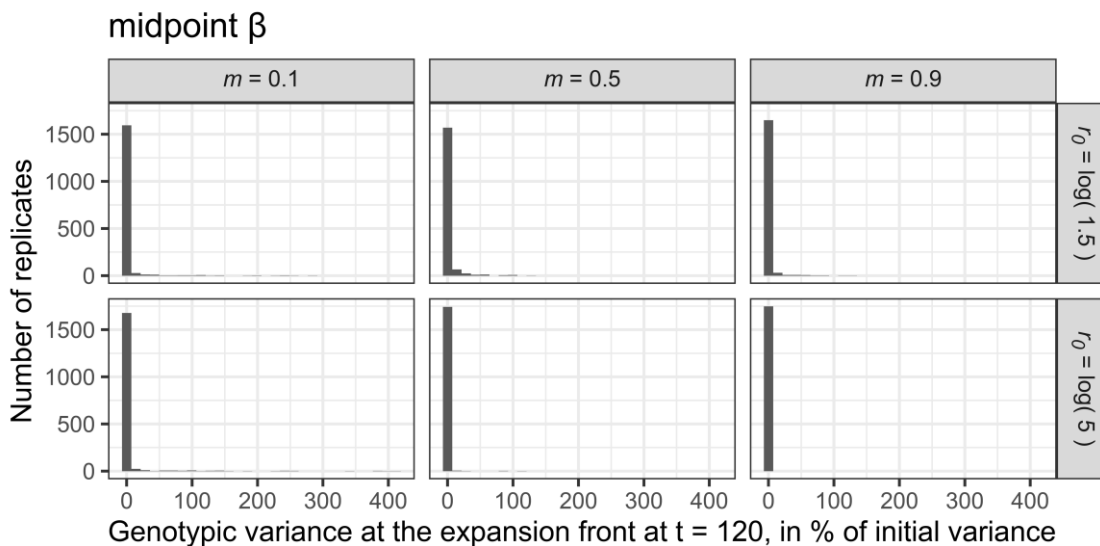
For all three dispersal traits, a very large majority of replicates have lost most if not all of their genetic variance by  $t = 120$  (**Figs S5.1, S5.2 and S5.3**), meaning there is limited to no potential for further evolution should the simulations run for longer. Note that **Figs S5.1 to S5.3** may still overstate the remaining potential for evolution: indeed, disruptive selection may lead to replicates where the final variances are still high, even higher than initial variances, and yet there are no further opportunities for selection.



**Figure S5.1.** Distribution of the remaining genetic variance in  $\logit(d_{max})$  at the expansion front at the end of the expansion. The values displayed are weighted averages of the patch-level variances, with the front defined as in **S4**. Only replicates that started with non-zero genetic variance in  $\logit(d_{max})$  are displayed.



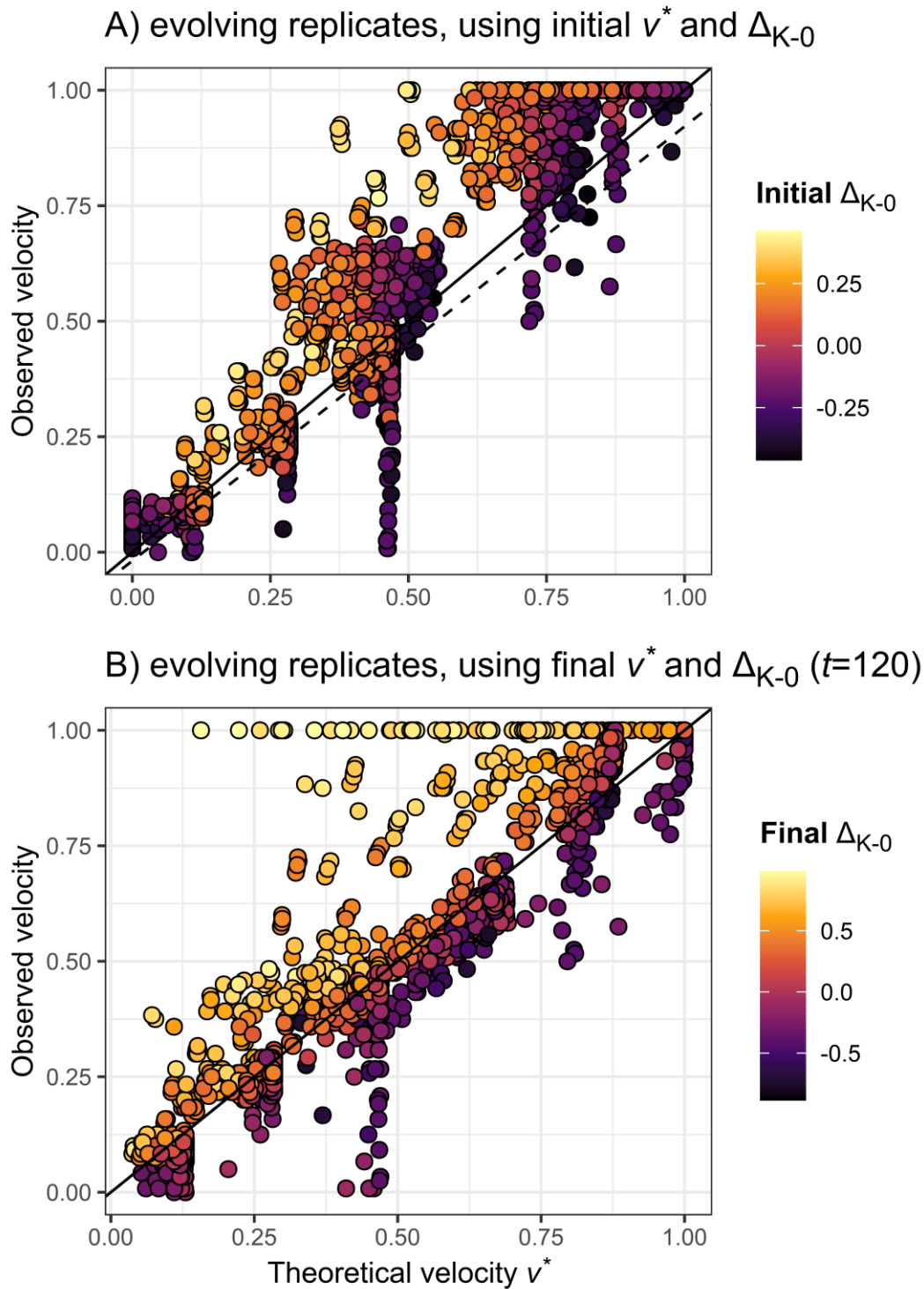
**Figure S5.2.** Distribution of the remaining genetic variance in the relative slope  $\alpha$  at the expansion front at the end of the expansion. The values displayed are weighted averages of the patch-level variances, with the front defined as in **S4**. Only replicates that started with non-zero genetic variance in  $\alpha$  are displayed.



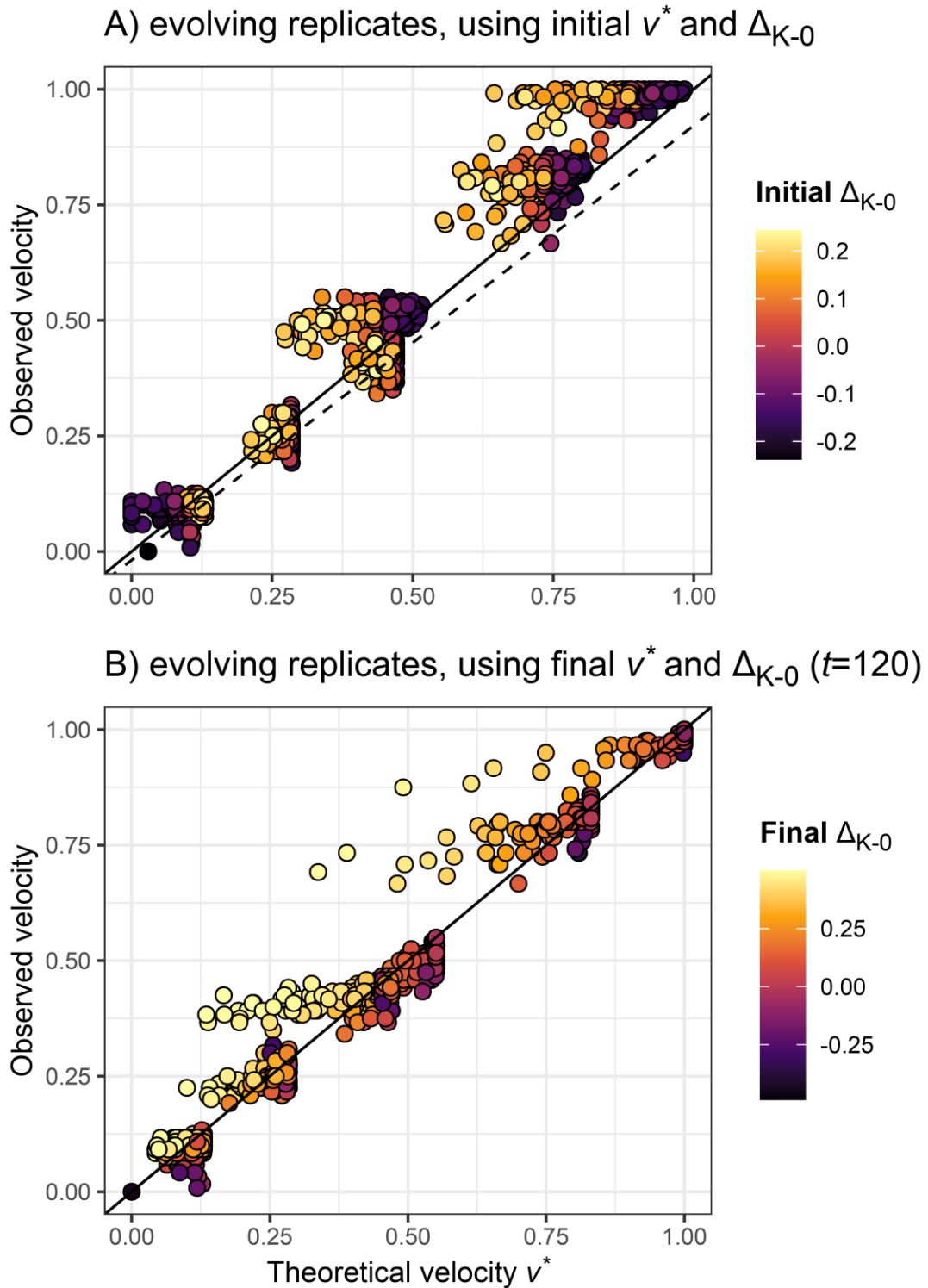
**Figure S5.3.** Distribution of the remaining genetic variance in the midpoint  $\beta$  at the expansion front at the end of the expansion. The values displayed are weighted averages of the patch-level variances, with the front defined as in **S4**. Only replicates that started with non-zero genetic variance in  $\beta$  are displayed.

## S6 - Velocities in replicates with evolution, split based on whether $d_{max}$ can evolve or not

Here we provide versions of **Fig. 4** of the main text, but this time by separating replicates where the maximal dispersal rate can (**Fig. S6.1**) or cannot (**Fig. S6.2**) evolve. We see that the qualitative conclusions we present in the main text apply to both subsets similarly.



**Figure S6.1.** Relationship between observed expansion velocities and expected theoretical velocities  $v^*$ , in expansions where the maximal dispersal rate  $d_{max}$  was allowed to evolve (whether or not density-dependence traits were allowed to). In (A),  $v^*$  and dispersal density-dependence  $\Delta_{K-0}$  are both calculated based on the initial distribution of dispersal traits, as in **Fig. 3** of the main text; in (B) they are instead calculated based on traits at the range front after evolution, at the end of the simulated expansion. Each replicate is coloured according to its value of dispersal density-dependence (note the different scales in (A) and (B)). The full straight lines correspond to  $y = x$ , the dotted line in (A) is the linear regression from **Fig. 3B** of the main text, i.e. for the replicates with  $\Delta_{K-0} = 0$  only in the absence of evolution.

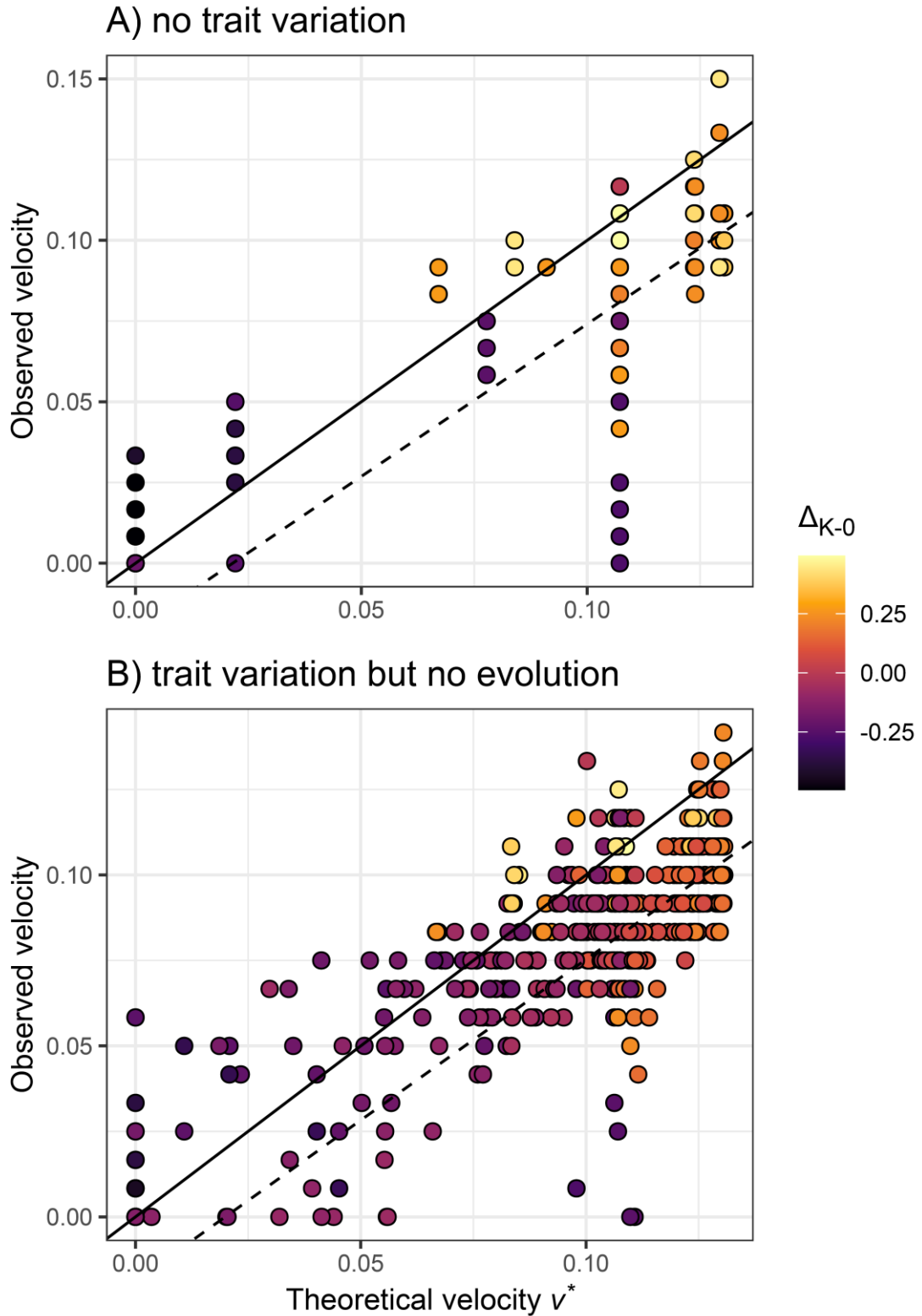


**Figure S6.2:** Relationship between observed expansion velocities and expected theoretical velocities  $v^*$ , in expansions where evolution was possible but only density-dependence traits ( $\alpha$  and  $\beta$ ) were allowed to evolve. Legend is otherwise identical to **Fig. S6.1**.



## S7 - Relationship between velocity and density-dependence when costs are high and fecundity low

We reproduce here a subset of the main text **Fig. 3**, focusing only on replicates with low fecundity and high dispersal mortality (**Fig. S7.1**). We show that in this subset, and contrary to the whole dataset, we do not find the relationship between expansion velocity and density-dependence that is expected from theory; that is, high  $\Delta_{K-0}$  do not lead to consistently higher velocities than expected from their  $v^*$ . The absence of a key pattern from pushed expansion theory is to put in perspective with a similar absence regarding genetic diversity (see main text **Fig. 5**).



**Figure S7.1.** Relationship between observed expansion velocities and expected theoretical velocities  $v^*$ , in the absence of trait evolution and for replicates with low fecundity ( $r_0 = \log(1.5)$ ) and high dispersal mortality ( $m = 0.9$ ). Each replicate is coloured according to its value of dispersal density-dependence. The full straight lines correspond to  $y = x$ , the dotted line are linear regressions for the replicates with  $\Delta_{K-0} = 0$  only (using all fecundity and mortality values, as in **Fig.3** of the main text).

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