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CONCEPT

Experimental evolution of dispersal: Unifying theory, experiments and natural systems

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Abstract

1. Dispersal is a central life history trait that affects the ecological and evolutionary dynamics of populations and communities. The recent use of experimental evolution for the study of dispersal is a promising avenue for demonstrating valuable proofs of concept, bringing insight into alternative dispersal strategies and trade-offs, and testing the repeatability of evolutionary outcomes.
2. Practical constraints restrict experimental evolution studies of dispersal to a set of typically small, short-lived organisms reared in artificial laboratory conditions. Here, we argue that despite these restrictions, inferences from these studies can reinforce links between theoretical predictions and empirical observations and advance our understanding of the eco-evolutionary consequences of dispersal.
3. We illustrate how applying an integrative framework of theory, experimental evolution and natural systems can improve our understanding of dispersal evolution under more complex and realistic biological scenarios, such as the role of biotic interactions and complex dispersal syndromes.

Nicky Lustenhouwer and Felix Moerman contributed equally to the work.

KEYWORDS
dispersal, dispersal syndromes, evolutionary trade-offs, experimental evolution, metacommunities, metapopulations, movement

1 | INTRODUCTION

Dispersal, generally defined as the movement of an individual from its place of birth to its place(s) of reproduction, is an integral part of a species' life history (Ronce, 2007). Dispersal traits often have a genetic basis (Saastamoinen et al., 2018) and are subject to considerable selection (Lowe & McPeek, 2014) with costs and benefits to the dispersing individual (Bonte et al., 2012; Bonte & Dahirel, 2017; Clobert et al., 2012). Dispersal traits not only differ between populations, but genetic and environmental linkages to other traits (i.e. joint selection on dispersal and adaptation to local environmental conditions) also generate heterogeneity within populations (Clobert et al., 2012). Given the strong impact of dispersal on the ecological dynamics of spatially structured systems (Bowler & Benton, 2005; Luo et al., 2022), evolutionary changes in dispersal have the potential to induce strong eco-evolutionary feedbacks. For example, dispersal evolution may alter metapopulation dynamics (Hanski et al., 2006; Jacob et al., 2019), population expansion rates (Miller et al., 2020; Nadeau & Urban, 2019), species interactions (Nørgaard et al., 2021; Phillips & Shine, 2006), local adaptation (Moerman et al., 2020; Tusso et al., 2021), and the evolution of niche width (Friedenberg, 2003). Yet disentangling the causes and consequences of dispersal evolution has often proven difficult in natural systems, due to the spatiotemporal scale of dispersal, the lack of replicability and the presence of confounding factors.

These limitations may be overcome through well-designed experimental evolution studies, that allow isolating ecological (e.g. population dynamics, species interactions, dispersal) and evolutionary (drift, gene flow, selection, mutation) processes in order to study their effects on the evolution of a given trait of interest (Bailey & Bataillon, 2016; Chevin, 2011; Kawecki et al., 2012; Schlötterer et al., 2015; Van den Bergh et al., 2018). Recently, this approach has also been applied to dispersal, demonstrating that different dispersal traits may evolve, that dispersal behaviour can be altered by population density and relatedness (Bitume et al., 2013), and that dispersal evolution can accelerate range expansion (Fronhofer, Gut, et al., 2017; Mishra et al., 2020; Ochocki & Miller, 2017; Van Petegem et al., 2018; Weiss-Lehman et al., 2017).

Despite this progress, the potential for experimental evolution to advance dispersal research is constrained by several challenges. Here, we outline how to mitigate these constraints by (i) identifying the possibilities and challenges of using experimental evolution to study dispersal; (ii) advocating a conceptual framework integrating experimental evolution, theoretical modelling and studies of natural systems; and (iii) proposing recommendations for future experimental evolution studies of dispersal.

2 | HOW (NOT) TO USE EXPERIMENTAL EVOLUTION TO STUDY DISPERSAL

2.1 | Possibilities

A main benefit of experimental evolution is the possibility to infer causation by isolating individual factors and processes to study their effects on evolutionary changes in a systematic and replicated manner. Dispersal evolution experiments include studies investigating two-patch systems (Friedenberg, 2003; Tung, Mishra, Shreenidhi, et al., 2018), linear arrays (Fronhofer & Altermatt, 2015; Mortier et al., 2021; Weiss-Lehman et al., 2017; Williams et al., 2016), metapopulations (De Roissart et al., 2015; Fronhofer et al., 2014; Masier & Bonte, 2020), and meta-communities (Nørgaard et al., 2021); see also Larsen and Hargreaves (2020) for an overview of experimental landscapes. In each experimental landscape, the available habitat (e.g. number of patches), population density, environmental conditions or species interactions can be manipulated to study how modulators such as landscape fragmentation (De Roissart et al., 2016; Fronhofer et al., 2014; Masier & Bonte, 2020; Williams et al., 2016) or environmental gradients (Fronhofer, Nitsche, et al., 2017) affect dispersal and its eco-evolutionary consequences. Further, by experimentally shuffling individuals, experimental evolution studies can effectively partition spatial (e.g. spatial sorting of individuals due to dispersal ability) vs. temporal (e.g. drift, density-dependent selection) contributors to dispersal evolution (Ochocki & Miller, 2017; Weiss-Lehman et al., 2017) and control for kinship structure. While such experiments may not be suitable to answer all questions related to the evolution of dispersal, they are especially useful in four key ways (further explored in Box 1 with representative studies):

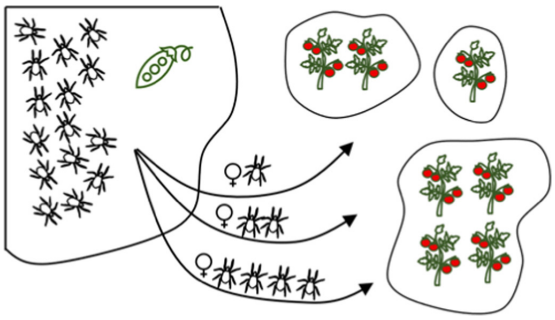
1. Certain dispersal processes, such as range expansions and extinction/colonization events are practically infeasible or too disruptive to experimentally manipulate in nature, making experiments ideal tools for simulating these processes (e.g. Alzate et al., 2019).
2. Experimental evolution studies are very effective as 'proof of concept' studies to test theoretical predictions related to the evolution of dispersal (e.g. Friedenberg, 2003; Ochocki & Miller, 2017; Williams et al., 2016), demonstrating experimentally to which extent certain eco-evolutionary processes occur and may apply to real-world systems.
3. Evolution experiments can yield valuable insights about traits under selection, correlated evolutionary responses, and the role of trade-offs in governing trait evolution (e.g. De Roissart et al., 2016; Van Petegem et al., 2018).

BOX 1 Key advantages of using experimental evolution to study dispersal.

Here we illustrate the four advantages of experimental evolution outlined in Section 2 with example studies.

1. Landscape design and dispersal

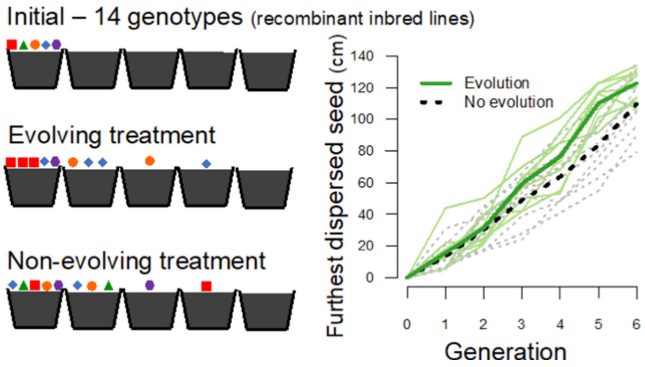
Experiments allow for manipulation of landscape features and dispersal rates or routes that would be intractable in nature (Larsen & Hargreaves, 2020). For instance, Alzate et al. (2019) used an island biogeography design where spider mites adapted to pea plants on the 'mainland' (stock) dispersed at different rates (number of females transferred) to islands of different sizes (number of tomato plants). The study focussed on the effects on population dynamics (colonization, extinction) and adaptation to the new host plant, but could be extended with mite dispersal morphology and behaviour



Experimental design used by Alzate et al. (2019). Mites were transffered at rate of 0.5, 1, or 2 females per week to 'islands' of 1, 2, or 4 tomato plants

2. Providing proof of concept

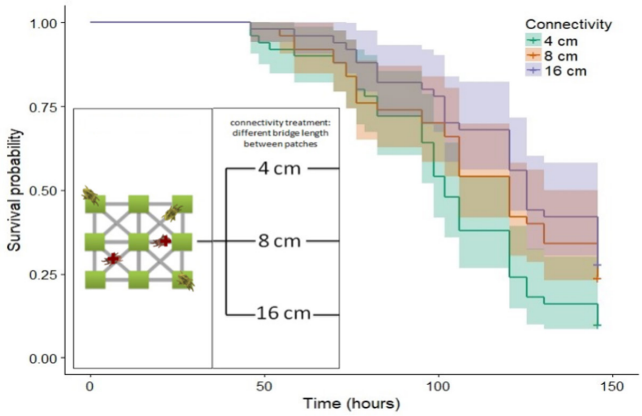
Experimental evolution has provided 'proof of concept' that evolution can accelerate range expansion (Ochocki & Miller, 2017; Weiss-Lehman et al., 2017; Williams et al., 2016). For example, Williams et al. (2016) created replicated experimental mesocosms with *Arabidopsis thaliana*, where each generation dispersed into a linear array of pots. In the nonevolving treatment, a replacement array was created with seeds sown at the same density and location, but with equal frequencies of the 14 starting genotypes (left panel, different coloured symbols). By comparing the furthest extent between the evolving and non-evolving treatments, they could quantify the extent to which evolution increased the speed of range expansion (right panel) and characterize which traits contributed



Left: experimental design with symbols indicating different genotypes. Right: furthest extent of evolving (green) and non-evolving (black) replicate invasions, with mean values in bold (from Williams et al., 2016, reprinted with permission from AAAS)

3. Unexpected insights into evolution

By allowing dispersal and population dynamics to play out freely within the landscape, experimental evolution studies often find emerging insights into selection on more than just emigration traits but also on other stages of dispersal and life histories. For instance, using mite experimental metapopulations, De Roissart et al. (2016) found metapopulation structure not to induce the evolution of emigration rates, but to impose complex but adaptive changes in developmental time, fecundity and sex ratio (Bonte & Bafort, 2019). Similarly, experimental range expansions showed spatial sorting of reproductive traits to prevail over dispersal, but kin competition to overrule any trait evolution (Van Petegem et al., 2018). Connectivity loss in experimental metapopulations lead to the evolution of dispersal costs rather than increased emigration rates or dispersal distance (Masier & Bonte, 2020)

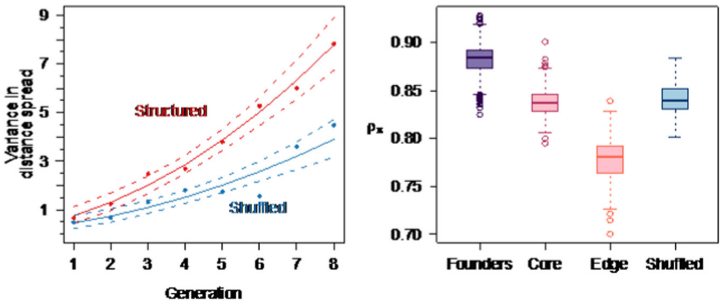


Changing connectivity in experimental spider mite metapopulations did not lead to the expected evolution of dispersal. Rather, dispersal costs evolved such that they equalized dispersal across the different connectivity treatments (from Masier & Bonte, 2020)

Here we illustrate the four advantages of experimental evolution outlined in Section 2 with example studies.

4. Quantifying variability

Variability among replicates can be studied at both the phenotypic and genomic level, which is particularly useful due to the large role of drift in range-expanding populations (Slatkin & Excoffier, 2012). Weiss-Lehman et al. (2017) used experimental microcosms of red flour beetles to test the role of spatial evolution on variability in expansion outcomes. In one treatment, beetles within a landscape were spatially randomized ('shuffled') each generation to remove any role of spatial evolution. After 8 generations, the non-shuffled landscapes ('structured') showed almost twice the variability in expansion distances of the shuffled landscapes. Analysing genomic data from this experiment, Weiss-Lehman et al. (2019) further demonstrated increased genomic variability in edge populations of structured landscapes, mirroring the increased variability seen in spread rates



Left: Variance in distance spread through time of the structured and shuffled treatments. Right: Pairwise correlation in nucleotide diversity (ρ_π) of key beetle populations from the experiment (lower values correspond to greater variability among replicates). Figures reprinted with permission from Weiss-Lehman et al., 2017 (left), and 2019 (right), respectively

4. The replicated experimental design provides the opportunity to study the repeatability of dispersal evolution (direction, magnitude and rate of change) and to understand why certain evolutionary outcomes and processes are more predictable than others (Weiss-Lehman et al., 2019; Williams et al., 2019).

2.2 | Challenges

Although experimental evolution may provide exciting opportunities to study the evolution of dispersal, several challenges should be considered (see Figure 1 for an overview of strengths and weaknesses compared to studying dispersal using theory or natural systems). First, given the short timescales and small landscape involved, scaling inference to natural systems is a major challenge (Morales & Ellner, 2002). Spatial and temporal scales of evolution experiments should thus be carefully tailored to the focal species and its mode of dispersal to produce relevant and realistic results. These constraints of artificial landscapes are clearly reflected in the taxonomic bias of study species towards small, short-lived organisms (Figure 2). However, some study systems are better than others for addressing particular questions: whereas complex dispersal behaviours at the level of the individual (individual dispersal decisions, body-condition dependency of dispersal) may be studied more easily in larger organisms (arthropods and vertebrates), bacteria and protists may be better suited to study species interactions, population dynamics and underlying genetic mechanisms. We highlight specific research questions that eight different groups of taxa would be suitable for (algae, arthropods, bacteria, ciliates, fungi, nematodes, plants and vertebrates) in Figure 2.

Second, regardless of their spatial and temporal scale, experimental evolution studies typically take place in a controlled laboratory or semi-natural environment. Dispersal traits that are under selection in an artificial environment may not be the same traits selected in nature (e.g. ambulatory vs. aerial dispersal), and dispersal behaviour is inherently constrained by the spatial limits and conditions of the experimental setting. Trade-offs observed in the lab could evolve in an unexpected direction (Lustenhouwer et al., 2019) and key traits impacting or trading off with dispersal in nature could be missed altogether (Tung, Mishra, Gogna, et al., 2018). If the goal of an experiment is extrapolation to natural populations, it is therefore imperative to proceed with caution and critically evaluate the extent to which dispersal in the artificial environment reflects real dispersal. In Section 3, we discuss further approaches to scale inference to natural systems.

Similar to phenotypic data, identifying the genetic basis of dispersal from lab experiments may only be relevant if the same traits (and genes) are under selection in nature. However, genomic approaches combined with experimental evolution are well suited to elucidate more general patterns, such as the repeatability of genetic changes associated with dispersal evolution, or differences in genetic load across experimental landscapes (Bosshard et al., 2020). Small effective population size and founder effects are natural outcomes of dispersal dynamics at range margins that will magnify the role of genetic drift and impact future evolution. An important task when using

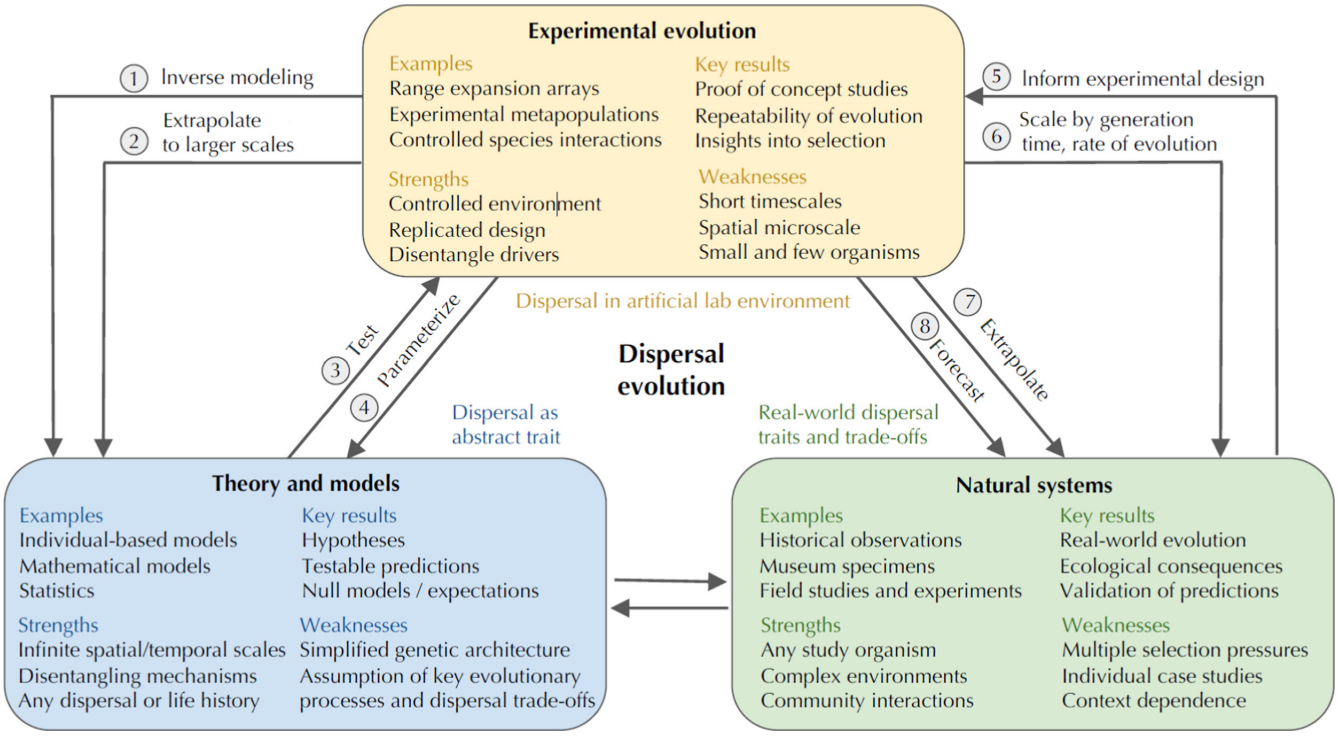


FIGURE 1 Interdisciplinary links between experimental evolution, theory and modelling, and natural systems that could advance the study of dispersal evolution, harnessing strengths and overcoming weaknesses of each approach. Numbered arrows are further discussed in Appendix 1 with relevant publications where available. Direct links between theory and natural systems are common but are outside the scope of this paper.

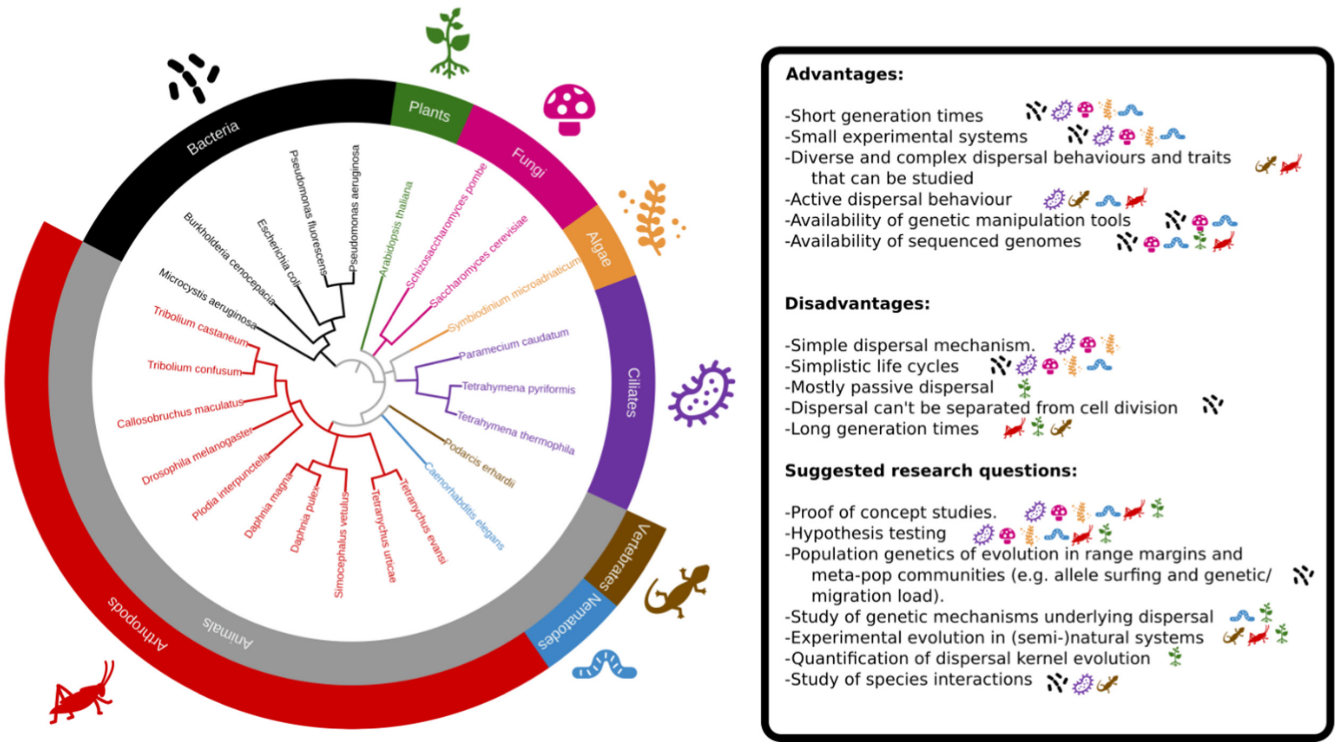


FIGURE 2 Taxonomic diversity of the species that have been used for the study of dispersal through experimental evolution. For each major taxonomic group, we list the main advantages and disadvantages for using an experimental evolution approach, as well as suggested research questions, for which the group may be well suited. Figure made using iTOL (Letunic & Bork, 2021).

experimental evolution to study the population genetics of dispersal is therefore to calibrate or monitor population sizes to ascertain that observed outcomes can be extrapolated to natural scenarios. Moreover, a small effective population size in the experiment will bias studies investigating the genetic basis of dispersal towards detecting loci with large effects. This issue arises due to the combination of the magnified role of drift in small experimental populations and the reduced statistical power to infer selection when replicate lineages adapt via different small effect alleles (Barton, 2022). This problem can be partly mitigated by genomic sequencing of temporal samples of evolving lineages, which improves statistical inferences of selection (Taus et al., 2017). Moreover, when applied to multiple replicate lineages, temporal sampling and sequencing can detect genetic linkage among outlier loci, further elucidating the targets of selection and providing insights into the repeatability of evolution (Barghi et al., 2019).

3 | FURTHER ADVANCING THE FIELD: LINKING THEORY, EXPERIMENTAL EVOLUTION AND NATURAL SYSTEMS

Scaling inference from dispersal evolution experiments to natural systems is arguably the most significant challenge impeding the critical step from proof-of-concept studies to forecasting the eco-evolutionary dynamics of dispersal in nature. Here, we highlight interdisciplinary research at the interface of theory, experiments and natural systems that may help bridge this gap and illustrate how future studies could explore dispersal evolution under greater biological realism (see Appendix 1 for a full list of suggested approaches).

3.1 | Integrating theory, models and experimental evolution

We see three main ways to improve integration between conceptual theory, modelling and evolution experiments. First, modelling and experimental evolution can be strengthened by mutually informing each study design—tailored experiments can validate analytical or statistical models, aid in model selection or evaluate predictability (Zilio et al., 2023; Figure 1, arrow 3 and 4). For example, theory has shown that high levels of genetic polymorphism in dispersal traits and/or high mutation rates can accelerate range expansion and alter trade-offs between reproductive output and movement/dispersal capacity (Elliott & Cornell, 2012; Morris et al., 2019). Experimental designs using replicate lineages with different starting levels of genetic variation in dispersal traits could test these predictions. In experiments with genetically tractable micro-organisms, putative mutations driving dispersal can even be re-engineered into the ancestor to establish a mechanistic causality (*cfr.* Fumasoni & Murray, 2020).

Second, simulation models can be used to tease apart complex dynamics, drivers and consequences of dispersal. Individual Based Models (IBMs) taking a bottom-up approach while explicitly considering genetic, ecological, and evolutionary processes, are a key example here (Bocedi et al., 2014; Rocha et al., 2021; Travis et al., 2011; Van Petegem et al., 2016; Weiss-Lehman & Shaw, 2022). Taking patterns observed in the experiments as inputs (e.g. dispersal between populations, population densities, relatedness, or genetic diversity), inverse modelling (Figure 1 arrow 1) can infer underlying eco-evolutionary processes that may be hard to observe or measure directly (Grindrod & Higham, 2010; Hartig et al., 2011; Soetaert & Petzoldt, 2010). For example, this approach has been applied to fit dispersal kernels (Sánchez et al., 2011), or to disentangle ecological and evolutionary drivers of dispersal behaviour (Bonte & Bafort, 2019).

Third, experimental data can be used to parameterize simulation models that incorporate larger populations and more complex environments, addressing the important challenge of scaling inference from experimental landscapes to natural systems (Figure 1 arrow 2). For example, metapopulation models could ask whether results (dispersal evolution, metapopulation dynamics) observed in a small, laboratory metapopulation will hold in larger, more extensive metapopulations with greater biological complexity (Kubisch et al., 2014).

3.2 | Extrapolating findings to natural systems

To assess whether patterns of dispersal evolution found in experimental landscapes can be extrapolated to more complex natural systems, direct comparisons to field data will be essential. Ideally, experimental results can be compared with documented time series of trait changes in natural populations (similar to the observed evolution in natural populations of Darwin finches; Grant, 2017). Barring such ideal data, observed outcomes of experimental evolution can be compared with trait changes in museum specimens or across phylogenetic transitions (*cfr.* methods used by Bagchi et al., 2021) and further linked to biogeographical changes in species distributions (Freedman et al., 2020; Figure 1 arrow 7). Resurrection experiments reviving historical populations through efforts such as project baseline (Etterson et al., 2016) provide another opportunity to validate results from evolution experiments with past and future evolutionary change in natural systems (Goitom et al., 2018).

An effective approach to link findings to natural systems is to perform evolution experiments in semi-natural systems such as mesocosms (Legrand et al., 2012; Stokstad, 2012) or even in replicated natural populations (Cheptou et al., 2008; Donihue et al., 2022; Hanski et al., 2006; Figure 1 arrow 7). By introducing selection lines from an evolution experiment (e.g. dispersive versus philopatric lines, or the leading and trailing edge from range expansion experiments) to a semi-natural system, it is possible to assess how evolutionary changes in dispersal affect population dynamics. De Bona et al. (2019) applied this approach in wild guppies, where individuals adapted to high levels of predation were transplanted across barrier waterfalls where predators are absent. This design mimics natural occurrences where guppies, but not their predators, have breached these barriers. The experimental introductions were used to assess

how density dependent dispersal evolves during a colonization event (De Bona et al., 2019). Dispersal evolution in this system can be further investigated with a combination of mark-recapture studies, mesocosms and common garden experiments examining the joint evolution of dispersal and life history across natural ecotypes.

3.3 | Integrative approaches addressing emerging questions

To illustrate how a combination of experimental evolution, theoretical predictions, modelling and field experiments may help answer major gaps in our understanding of dispersal evolution, we highlight hypothetical studies investigating dispersal evolution in the presence of two currently understudied factors: trade-offs between dispersal and other life history traits, and interspecific interactions (Figure 3). First, it is well-known that dispersal traits are often associated with life history, behavioural or morphological characteristics, resulting in dispersal syndromes (Clobert et al., 2012) that affect ecological processes such as population spread (Lustenhouwer et al., 2017). Consequently, evolutionary changes in dispersal may leave a legacy on other demographic parameters of the population (Lustenhouwer et al., 2019). Second, theory and experimental studies of dispersal evolution in spreading populations almost exclusively focus on a single species. However, the eco-evolutionary dynamics of dispersal will unfold in the context of (often strong) species interactions, especially during climate-mediated range shifts where entire species communities are reshuffled (Urban et al., 2012).

The potential for trade-offs and species interactions to fundamentally alter dispersal evolution is illustrated by a model simulating range expansion of species into a region occupied by a competitor (Burton et al., 2010), assuming a trade-off between dispersal ability, reproductive performance and competitive ability. In the absence of a competitor, selection favoured greater investment in dispersal at the expense of competitive ability. However, in the presence of a competitor, trade-offs constrained the evolution of increased dispersal at the expanding front. A second model by Kubisch et al. (2014) illustrated that the type of interaction occurring between two range expanding species (e.g. mutualistic vs competitive vs exploitative)

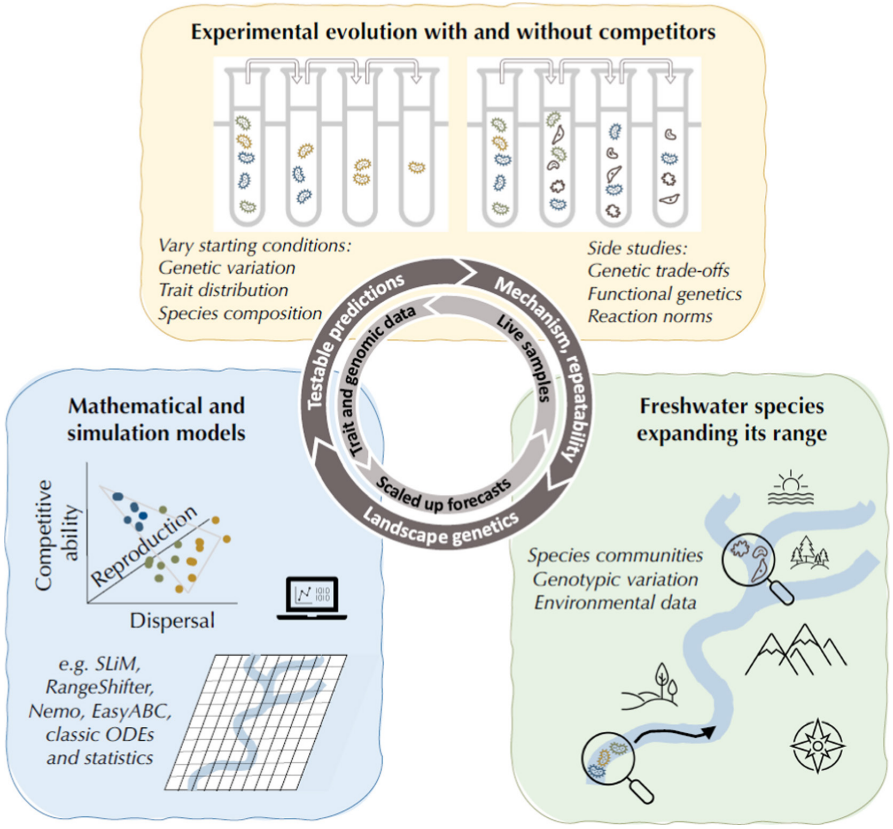


FIGURE 3 Example of a potential integrative approach between experimental evolution, natural systems and theory to study an imaginary protist species expanding its range along a river. A range of genotypes are sampled in the field, which vary along a trade-off (high dispersal- yellow genotype, high competitive ability-blue genotype, intermediate genotype- green). The focal species encounters novel competitors during range expansion, which are sampled downstream and used to set up experimental range expansions with and without competitors. Spatially explicit IBMs are parameterized with environmental and landscape genetic data from the field landscape, in combination with the relevant trade-off structure and population dynamics results identified in the evolution experiment. Modelling examples are from Haller and Messer (2019), Bocedi et al. (2021), Guillaume and Rougemont (2006), and Jabot et al. (Jabot et al., 2013, EasyABC).

can substantially change the dynamics and outcome of dispersal evolution across the expanding range.

Although dispersal evolution during range expansion in a multi-species context needs to be further explored theoretically, emerging predictions can already be tested using experiments where interacting species spread in micro- or mesocosms (Figure 3). The experimental tools at our disposal range from experimental communities of competing species (Matthiessen & Hillebrand, 2006) to complex meta-foodwebs (Altermatt et al., 2015; Carrara et al., 2012). Such resources allow us to ask how different types of interspecific interactions affect eco-evolutionary dynamics and whether the presence of interspecific interactions affects the predictability of evolutionary trajectories and demography.

On a final note, interdisciplinary studies are also a promising approach to examine (evolutionary changes in) dispersal plasticity under different environmental conditions (Campana et al., 2022). Meta-population experiments have recently shown that dispersal plasticity is impacted by top-down and bottom-up effects (Cote et al., 2022; Fronhofer et al., 2018) including potential consequences for meta-foodweb stability. Dispersal plasticity may also evolve along environmental gradients such as those experienced by range-expanding populations (Fitt et al., 2019). To test this hypothesis, experiments could be seeded with individuals from different parts of the range, based on genetic markers that can assess patterns of connectivity among populations and landscape resistance to dispersal (Dudaniec et al., 2022), using software such as Circuitscape (McRae & Beier, 2007) and Geneclass, (Piry et al., 2004). Individuals may also be reared under common garden conditions to establish how environmental variation affects dispersal. To forecast dispersal evolution in the context of natural communities, spatially explicit process-based models can be parameterised with the experimentally estimated vital rates, reaction norms and trade-offs, as well as with genetic data (e.g. heritability and amount of standing genetic variation in dispersal) and run under different scenarios (Figure 3).

4 | CONCLUDING REMARKS

Experimental evolution is a powerful tool to study the evolution of dispersal. Major experimental challenges can be overcome by addressing scaling issues (e.g. combining experiments with models to extrapolate results, scaling experimental findings to species with longer generation times), expanding the taxonomic range (i.e. use mesocosm or semi-natural experiments to include less well-represented species that are not suited to a traditional lab set-up), and carefully considering how population size affects the outcome of dispersal evolution in experimental and natural populations (see Appendix 1 for a detailed list of suggested methods and case studies). We argue the best way to do so is to reinforce links between experimental evolution, natural systems and theory/modelling, by, for example, using experimental evolution to validate analytical models, parameterize genetically explicit IBMs, or test the replicability of evolutionary changes observed in natural populations (Figure 3 and Appendix 1). Such an integrative framework will make it possible to design more realistic experimental evolution studies in the future to answer questions of increasing biological complexity—how dispersal evolves in the context of species interactions, environmental variation and genetic variation underlying dispersal in the natural world.

AUTHOR CONTRIBUTIONS

Luca Börger and David Berger conceived the idea for the concepts manuscript. Nicky Lustenhouwer and Felix Moerman wrote the manuscript, with input from all co-authors. All authors commented on and approved of the final version.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

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No new data was generated/analyzed for this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix 1. Suggested methodologies on how experimental evolution of dispersal can be linked to theoretical and empirical work, to advance our understanding of dispersal evolution. For each of the numbered arrows from Figure 1, we list several methodologies with a brief explanation and relevant studies.

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