

Research



Cite this article: Bestion E *et al.* 2024 Species interactions affect dispersal: a meta-analysis. *Phil. Trans. R. Soc. B* **379**: 20230127.

<https://doi.org/10.1098/rstb.2023.0127>

Received: 31 October 2023

Accepted: 6 March 2024

One contribution of 16 to a theme issue 'Diversity-dependence of dispersal: interspecific interactions determine spatial dynamics'.

Subject Areas:

ecology

Keywords:

context-dependent dispersal, metacommunity dynamics, predator–prey interactions, competition, host–parasite interactions, biotic interactions

Author for correspondence:

Elvire Bestion

e-mail: elvire.bestion@sete.cnrs.fr

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.25887136>.

Species interactions affect dispersal: a meta-analysis

Elvire Bestion¹, Delphine Legrand¹, Celina B. Baines², Dries Bonte³, Aurelie Coulon^{4,5}, Maxime Dahirel³, María Delgado⁶, Jhelam N. Deshpande⁷, Alison B. Duncan⁷, Emanuel A. Fronhofer⁷, Isabelle Gounand⁸, Staffan Jacob¹, Oliver Kaltz⁷, François Massol⁹, Erik Mathyssen¹⁰, Thomas Parmentier^{3,11}, Camille Saade⁷, Nicolas Schtickzelle¹², Giacomo Zilio^{5,7} and Julien Cote¹³

¹Station d'Ecologie Théorique et Expérimentale, CNRS, UAR 2029, Moulis 09200, France

²Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Canada M5S 3B2

³Terrestrial Ecology Unit (TEREC), Department of Biology, Ghent University, K.L. Ledeganckstraat 35, Ghent 9000, Belgium

⁴Centre d'Ecologie et des Sciences de la Conservation (CESCO), MNHN, CNRS, Sorbonne University, Paris, Concarneau 75005, France

⁵Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), University of Montpellier, CNRS, Montpellier 34293, France

⁶Biodiversity Research Institute (IMIB), CSIC/UO/PA, Campus de Mieres, Edificio de Investigación, Mieres, Asturias 33600, Spain

⁷ISEM, Université de Montpellier, CNRS, IRD, EPHE, Montpellier 34095, France

⁸Institut d'écologie et des sciences de l'environnement (iEES Paris), Sorbonne Université, CNRS, UPEC, CNRS, IRD, INRA, Paris 75005, France

⁹Institut Pasteur de Lille, University Lille, CNRS, Inserm, CHU Lille, U1019 - UMR 9017 - CIIL - Center for Infection and Immunity of Lille, Lille 59019, France

¹⁰University of Antwerp, Wilrijk 2610, Belgium

¹¹Research Unit of Environmental and Evolutionary Biology, Namur Institute of Complex Systems, and Institute of Life, Earth, and the Environment, University of Namur, Rue de Bruxelles 61, Namur 5000, Belgium

¹²Earth and Life Institute, UCLouvain, Louvain-la-Neuve 1348, Belgium

¹³Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), UMR 5300 CNRS-IRD-TINP-UT3, Université Toulouse III – Paul Sabatier, Bât. 4R1, 118 route de Narbonne, Toulouse 31062, France

ORCID EB, 0000-0001-5622-7907; CBB, 0000-0002-6918-3648; DB, 0000-0002-3320-7505; MD, 0000-0001-8077-7765; MD, 0000-0002-3009-738X; ABD, 0000-0002-6499-2913; EAF, 0000-0002-2219-784X; IG, 0000-0002-0675-3973; SJ, 0000-0003-1956-9646; FM, 0000-0002-4098-955X; EM, 0000-0002-7521-9248; TP, 0000-0002-4082-0922; CS, 0000-0003-2368-9480; NS, 0000-0001-7829-5361; GZ, 0000-0002-4448-3118; JC, 0000-0002-4453-5969

Context-dependent dispersal allows organisms to seek and settle in habitats improving their fitness. Despite the importance of species interactions in determining fitness, a quantitative synthesis of how they affect dispersal is lacking. We present a meta-analysis asking (i) whether the interaction experienced and/or perceived by a focal species (detrimental interaction with predators, competitors, parasites or beneficial interaction with resources, hosts, mutualists) affects its dispersal; and (ii) how the species' ecological and biological background affects the direction and strength of this interaction-dependent dispersal. After a systematic search focusing on actively dispersing species, we extracted 397 effect sizes from 118 empirical studies encompassing 221 species pairs; arthropods were best represented, followed by vertebrates, protists and others. Detrimental species interactions increased the focal species' dispersal (adjusted effect: 0.33 [0.06, 0.60]), while beneficial interactions decreased it (−0.55 [−0.92, −0.17]). The effect depended on the dispersal phase, with detrimental interactors having opposite impacts on emigration and transience. Interaction-dependent dispersal was negatively related to

species' interaction strength, and depended on the global community composition, with cues of presence having stronger effects than the presence of the interactor and the ecological complexity of the community. Our work demonstrates the importance of interspecific interactions on dispersal plasticity, with consequences for metacommunity dynamics.

This article is part of the theme issue 'Diversity-dependence of dispersal: interspecific interactions determine spatial dynamics'.

1. Introduction

The dynamics of local and regional communities result from the distribution and abundance of interacting species [1]. At a local scale, the strength and direction of these interactions affect coexistence and community dynamics. At a regional scale, local communities are linked by the dispersal of potentially interacting species among local habitats [1]. Species dispersal links local and regional community dynamics (i.e. metacommunity dynamics) and influences local population dynamics and community composition [1]. A better understanding of the dispersal process, and its eco-evolutionary drivers, is therefore crucial for understanding its influences on community dynamics at different landscape scales [2,3].

Theoretical and empirical studies have demonstrated that dispersal depends on the experienced and anticipated biotic and abiotic environment, referred to as context-dependent dispersal [4–6]. Indeed, organisms do not move randomly through a landscape; the propensity, direction and distance moved can be plastically adjusted to the local abiotic and biotic conditions encountered before and while moving [4]. Theory shows that individuals can disperse adaptively because emigration and immigration could depend on the expected fitness in the arrival patch available for colonization relative to the fitness expected in the departure patch [7]. The theory also predicts that such context-dependent dispersal can evolve in spatially and temporally heterogeneous habitats [8]. Further, the evolution of context-dependent dispersal depends on the reliability and cost of information acquisition [9]. Among the many factors theoretically found to drive the evolution of context-dependent dispersal are patch size and quality, as well as fluctuation in population density or kin competition [8,10,11]. Such context-dependent dispersal can itself affect eco-evolutionary dynamics, including source–sink population dynamics or species ranges, and can further affect metacommunity functioning and stability through changes in species abundances and community composition [12].

The direction and strength of local interactions are major determinants of fitness and therefore expected to be among the most important proximal drivers of dispersal [3]. Bottom-up and top-down controls of dispersal are now well documented (e.g. [13]) and evidence is accumulating for the context-dependency of dispersal in other types of species interactions (e.g. interspecific competition, host–symbiont interactions [14,15]). Furthermore, certain species can only disperse through other species' movements, such as animal-dispersed seeds or symbionts dispersing through their hosts' movements [16,17]. Despite the importance of species interactions, it remains unclear how their nature actually shapes dispersal plasticity within and among taxonomic groups. After a systematic review of the existing literature, we performed a meta-analysis of published studies investigating species interactions as proximal drivers of dispersal to discuss the potential consequences for metacommunity dynamics and identify important research gaps with respect to the development of a more mechanistic metacommunity theory. To do so, we extracted data from 118 observational and experimental studies focusing on either the emigration stage, the transience stage or the full dispersal process from emigration to immigration, excluding studies focusing only on colonization. We focused on mobile and actively dispersing species, and thus excluded studies on sessile or passive dispersing species (e.g. plants). Our database, which was taxonomically biased towards animals (essentially arthropods and vertebrates), encompassed 221 species pairs and six types of interactions experienced by the focal species, i.e. detrimental interactions with predators, consumers or parasites, and beneficial interactions with resources, hosts or mutualists. We quantified how the presence/absence or the abundance of an interacting species influenced the dispersal of a focal species through plastic changes across interaction types and identified key moderators of this context-dependent dispersal (figure 1). We especially addressed the following questions:

(a) Does the impact of interacting species on dispersal depend on the nature of species interactions?

Species interactions can be first described through their general effects on the focal species (figure 1). Beneficial interactors are resources, hosts and mutualists that should increase the fitness of the focal species. Detrimental interactors are predators, parasites and competitors that should decrease the fitness of the focal species. If dispersal depends on fitness expectations [7], detrimental interactions, endured or expected, should increase species dispersal propensity away from local habitats containing the interactor, while the opposite should be true for beneficial interactions, even if this effect should depend on species' ecological traits (see the following text). Evolution of such interaction-dependent dispersal has been theoretically and empirically shown for predator–prey, host–parasite and interspecific competition interactions [6,14,18], showing for example that models of density-dependent dispersal could be transferred from a single species to a multi-species context [14].

Beyond their expected effects on fitness, different species interactions might actually lead to different dispersal strategies to mitigate fitness effects (figure 1). Some interaction types might not be efficiently mitigated by species movements or might induce high dispersal costs. Dispersing away from local habitats might therefore fail to improve expected fitness. For example, interspecific competition negatively affects a competitor's fitness by reducing acquired energy, thus increasing the reward to be gained from moving while reducing the energy available for movement. Thus, it may result in more complex—quadratic

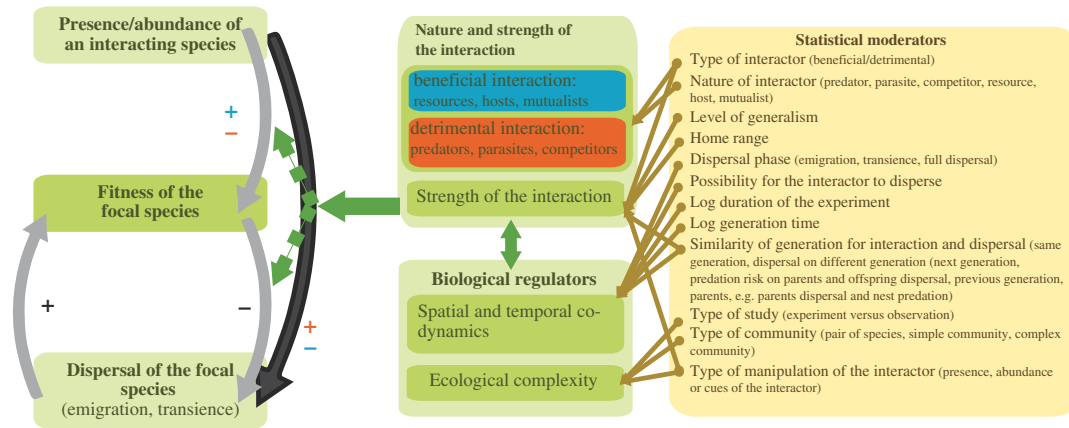


Figure 1. The relationships between species interactions and dispersal. The dispersal of a focal species depends upon its biotic context, especially if the presence/abundance of an interacting species affects its fitness (grey arrows). In this meta-analysis, we extracted data from the literature to determine how the presence/abundance of the interacting species affects the dispersal of a focal species (black arrow). The relationship between interacting species' presence/abundance and dispersal depends on the nature and strength of the biological interactors. Detrimental interactors such as predators, parasites or competitors (in red) negatively affect the fitness of the focal species (red – sign on the grey arrow). Because there is a negative relationship between fitness and dispersal (black – sign on the grey arrow), they should thus positively affect its dispersal (red + sign on the black arrow). On the other hand, beneficial interactors such as resources, hosts and mutualists (in blue) should positively affect the fitness (blue + sign on the grey arrow), and through the negative link between fitness and dispersal (black – sign), negatively affect dispersal (blue – sign on the black arrow). The effect of these interactions should depend on numerous biological regulators, related to the spatio-temporal co-dynamics and the ecological complexity, which affect the strength of interaction between species and thus the strength of interaction-dependent dispersal (green arrows). We translated these biological regulators into a number of statistical moderators (gold arrows) to explain the dependency of dispersal on the presence of an interacting species. By testing for these moderator effects on the relationship between the presence/abundance of the interacting species and dispersal of the focal species (gold and green arrows), we attempted to make inferences about the way fitness is affected by the interacting species and the way it affects the dispersal of the focal species (green arrows).

or threshold-like—relationships between the expected fitness consequences of interactions, the actual strength of interactions and emigration propensity. Such relationships may vary with energy availability, movement costs and niche overlap between interacting species. Complex effects of competition have been found for intraspecific competition, with a systematic review showing that intraspecific density could either positively, negatively or nonlinearly affect dispersal [19]. Predation risk, on the other hand, intrinsically reduces prey fitness, making movement out of habitats highly rewarding but also often highly risky [20], with potentially opposite effects on dispersal depending on the risk level. Similarly, by diverting their hosts' resources, parasites can constrain their dispersal [21]. However, hosts may increase their dispersal propensity to escape an infested habitat [15], and parasites themselves can manipulate their hosts' dispersal to increase contact rate and the transmission of parasites [21]. We expect the interaction type to modulate the dependency of dispersal to interaction strength (i.e. interaction-dependent dispersal) and this effect should further depend on a suite of biological and ecological factors (figure 1).

(b) Does the dispersal response depend on the spatiotemporal dynamics of interacting species?

Dispersal is not always the best strategy to escape adverse interactions or to search for beneficial ones. Its efficiency should depend on temporal synchrony and spatial overlap of interacting species ([6], figure 1). First, dispersing may not lead to changes in encounters with an interacting species if that species has a wider spatial distribution. In such a case, dispersing individuals would bear more of the energy, time and opportunity costs of moving [22] than its benefits. For example, predators often have larger home and movement ranges than their prey [23,24] but are also found at lower densities. Prey species may thus need to disperse over longer distances to reduce predation risk. However, transience is a highly vulnerable stage when prey are exposed to predators [20], which may result in predators having different impacts on the focal prey species' emigration phase or transience, depending on the spatio-temporal dynamics [13] and the asymmetry in space use between predator and prey. When dispersal does not efficiently influence the adverse or beneficial effects of interactions, species may opt for alternative mitigation strategies, such as switching their activity period or their microhabitat use. We first compared studies investigating interaction-dependent emigration (through emigration rate) and transience (through dispersal distance) for the different types of interactions. We expected interacting species to influence dispersal distances more than emigration probability when interacting partners differ in their spatial distribution (e.g. consumer–resource interaction). Following the same rationale, we expected stronger influences of interaction in (typically experimental) studies when only the focal species could disperse compared with cases where both species could disperse. Furthermore, we expected the relative home range of interacting species to affect the dispersal response (figure 1).

Second, the temporal dynamics of interacting species may modulate the efficiency of dispersal in mitigating species interactions. Interacting species may differ in (i) their daily and seasonal profiles of activity and (ii) the temporal autocorrelation of their population sizes [13]. For instance, in aphids, the evolution of delayed predator-induced dispersal, where predator presence induces the production of winged offspring, depends on the temporal correlation in predation risk [6]. We were not able to gather information on the daily and seasonal profiles of activity, but we investigated this temporal aspect by comparing studies in which the encounter with the interacting species and the dispersal responses occur within the same generation or

across different generations, as well as studying the impact of the duration of the experiment and of species' generation time (figure 1).

(c) Do the interaction strength and ecological complexity affect the dispersal response?

One species' impact on the dispersal of another interacting species may depend on their interaction strength [14] because interaction strengths should affect fitness expectations. Assessing interaction strength between species is a non-trivial endeavour, both for the researcher [25] and possibly for the interacting organisms, which may rely on several types of cues to determine it. The interaction strength perceived by a given individual may depend on various moderators, including the abundances of the interacting partners, the actual presence or the perception of cues, the niche overlap and generalism of interacting partners, as well as the overall ecological complexity. For example, we can expect cues of the presence of interacting species to elicit a weaker perception of interaction strength and a weaker dispersal response than the actual presence of the interactor. Conversely, the fear of predators has long been considered to have stronger impacts on prey than their actual presence and consumption [26]. The effect of interaction on species fitness and dispersal may further depend on community complexity (figure 1), i.e. the diversity of interacting partners within the same and across interaction types. Multiple host species for a single parasite may for example decrease the interaction strength with each host species through a dilution effect that decreases disease risk [27]. A similar prediction can be made for any interaction type. Comparing studies using a two- or a multi-species network may therefore provide information on the role of interaction strength, with the prediction that a design with pairs of species may overestimate the dependency of dispersal on interaction strength. Similarly, experimental studies may reduce ecological complexity but have better detection of interaction strength than observational studies. The strength of interaction may also depend on the level of generalism of interacting species, with more specialist interactors likely having stronger impacts on the focal species and hence on their dispersal. Most of the studies investigating interaction-dependent dispersal lacked an assessment of interaction strength between species; however, several aspects of the environmental context could be used as a cue of interaction strength. We thus investigated modulating effects of metrics related to community complexity, types of manipulation (i.e. cues versus actual presence or abundance of interacting species), type of studies (observational versus experimental) and level of generalism of both the focal and interacting species in dispersal studies. Furthermore, we used a second literature search to estimate expected interaction strengths between pairs of species present in our database, which was possible for a majority of species pairs but involved a large variation between the ecological contexts of dispersal and interaction strength studies.

2. Methods

(a) Systematic literature review

We compiled a database of existing studies quantifying how the presence/absence or the abundance of an interacting species influences the dispersal of a focal species. Our database focused on actively dispersing species to examine the relationship between the dispersal response and the interaction strength, but not the numerical and behavioural effects of dispersal vectors. We defined active dispersal as dispersal in which the organism either actively moves during the transience phase or actively initiates the emigration phase (e.g. ballooning dispersal in which the wind is the vector of the transience but the organism actively initiates dispersal by its tiptoeing behaviour [28], or dispersal by a biological vector where the organism actively climbs on top of the vector [29]). Organisms that are passively picked up and carried by the wind or a dispersal vector, such as most cases of seed dispersal, were thus excluded. In addition, we excluded studies that focused only on the immigration/colonization phase of dispersal because the habitat choices of focal species that depended on local interactors (the purpose of the present study) could not be distinguished from the viability of focal species depending on local interactors (i.e. colonization success). However, immigration decisions with respect to species interaction are expected to mirror emigration decisions and so we expect our conclusions to apply to immigration decisions as well [5]. In the end, our literature search included emigration decisions, dispersal distance, the timing of dispersal and any type of species interactions (interspecific competition, consumer–resource interactions, parasitism and mutualism). electronic supplementary material, figure S1, shows the process of study identification, selection and the data extracted from each relevant article. We aimed to follow the preferred reporting items for systematic reviews and meta-analyses (PRISMA [30]) as well as the framework's extension for ecology and evolutionary biology [31].

We conducted the literature search on Web of Knowledge in October 2021 (timespan: 1975–2021) including keywords for (i) dispersal in the title (dispers* OR migrat* OR emigrat* OR immigrat* OR colonis* OR coloniz* OR nomadi*) and excluding other types of movements, i.e. seasonal migration (fall, autumn, spring migration, vertical migration, catadrom*, anadrom*), human migrations (i.e. refugees, international migration, domestic migration, human migration, asylum, illegal) or particle dispersion, and (ii) species interaction in the title and/or subject (predat* OR resource* OR prey* OR parasit* OR host* OR compet* OR facilitat* OR mutualis* OR cooperat* OR phore* OR commensal* OR interspeci* OR heterospeci* OR context* OR condition* OR metacommunit* OR 'mutual inhibition' OR ammensalis* OR symbio*). We focused on the Web of Science core collection and filtered results by Web of Science categories relevant to our broad thematic; see electronic supplementary material, Box S1, for a full description of the keywords and categories. During the search process, we checked for the inclusion of known relevant articles in the database to ensure that we did not miss important articles. The search yielded 21 499 articles.

(b) Inclusion criteria

We examined each title and abstract to determine whether articles met the criteria for inclusion in our overview of the literature with the METAGEAR package v.0.7 [32] in R. Criteria for inclusion comprised (i) the presence, abundance or density of an interacting species was quantified and varied experimentally or in observational studies, (ii) the rate of emigration or the dispersal distance or another dispersal metric of a focal species that was quantified in different contexts of species interactions, (iii) the effect of a single interacting species on a focal species can be isolated when more than two species were studied, and (iv) the two species were interacting species in natural environments, excluding artificial biotic elements (e.g. unnatural resource or predator species). At times, the title and abstract were too vague to positively assess these three criteria of inclusion, and the articles were kept for further detailed reading of the text; they could be thus excluded in a second filtering session. All examiners went through a training process in which they screened abstracts and titles for a set of 150 articles that were pre-selected by the first author to contain studies that were both easy and more difficult to rate as relevant or irrelevant. We estimated the inter-examiner accuracy, yielding a Cohen's κ of 0.40, corresponding to a fair to moderate agreement [33]. This first batch allowed us to identify points of misunderstanding and better explain the criteria for selecting an article. Then, all examiners went through 70 new articles that were deemed especially difficult to rate and we checked for potential discrepancies. Although the batch was more difficult, inter-examiner accuracy increased ($\kappa = 0.43$). This second batch allowed us to clarify the final difficult points before splitting the abstracts between examiners so that each examiner read and rated ~1100 abstracts. During this second phase, inter-examiner accuracy was examined again on 20 articles per reviewer, yielding a κ of 0.73, which is considered a substantial agreement [33]. The filtering process led to a selection of 1539 studies from the original search that fitted the scope of this overview.

(c) Effect size extraction

Selected articles were reviewed in full to determine whether they fit our inclusion criteria, contained relevant data, and whether the results were presented with sufficient clarity to extract effect sizes (electronic supplementary material, figure S1). During this step, we excluded (i) studies in which the focal species dispersed passively and in which there was no active choice to emigrate, (ii) studies focused on the colonization process only, keeping studies on emigration, transience, or those that monitored the full dispersal process; (iii) studies in which the second species did not interact with the focal species; and (iv) studies in which the effect of an interacting species on the dispersal of the focal species was compared to a control with a second interacting species instead of no interacting species or different abundances of interacting species. This step led to the further exclusion of 1420 articles from the first search. In the final set of 119 studies, we extracted 403 effect sizes and collected information on several moderators to investigate our questions of interest (see electronic supplementary material, reference list). Data to calculate effect sizes were extracted preferentially from raw data when available, from figures using the *juicer* v. 0.1 R package [34], or directly from the paper (tables or main text). Effect sizes were calculated with *esc* v. 0.5.1 [35] and *effect size* v. 0.8.5 R [36] packages and computed as Hedges' d from pairs of means (282 effect sizes, es), or converted to Hedges' d from contingency tables (41 es), correlations (15 es), log odds ratios (19 es), from different test metrics reported in the text (46 es, calculated from χ^2 , F or t values, non-parametric test values, or partial η^2 from ANOVA-like tables), see [37–43] and electronic supplementary material, table S1, for a list of equations used. Depending on the study, the sign of the effect sizes had to be reversed to be comparable among studies (e.g. effect sizes of remaining rate instead of departure rate, time to dispersal where increased time suggests decreased dispersal propensity). When studies presented several effect sizes for the same dispersal metric, e.g. when the impact of the interacting species was crossed with the effect of another biotic or abiotic factor, we combined groups following [38] when there was no significant interaction between the effect of species interaction and the second factor. Several effect sizes were missing variance information ($n = 16$), thus we used an imputation procedure to fill in back-transformed variance from the predicted values from a model of $\log(\text{variance})$ by $\log(\text{study sample size})$. Furthermore, several effect sizes had an extremely large variance ($n = 6$ es with variance > 2), which led to instability in meta-analysis results so we decided to drop these effect sizes, leading to a final sample size of 397 effect sizes from 118 studies (exclusion of one study).

Aside from the effect sizes, we extracted several aspects of the experimental design (electronic supplementary material, table S2). First, we included the taxonomic identity for the focal taxon and interacting taxon, i.e. either the species or the taxonomic level described (e.g. genus, family, order; for simplicity, we will refer to the focal species and interacting species throughout the text, but higher taxonomic levels may be used depending on the study; electronic supplementary material, table S2). Second, we added the type of interactor, i.e. whether the interacting species is a detrimental interactor such as a predator, resource, competitor or a beneficial interactor such as a host, parasite or mutualist (see the details of each category in electronic supplementary material, table S2). Third, we detailed the dispersal phase studied (emigration, transience or full dispersal process from emigration to settlement). Fourth, we included the type of manipulation (or variation in the case of observational studies) of the interactor: manipulation of presence versus abundance, manipulation of actual physical presence versus cues of presence, level of community complexity (pairs of species, simple community, complex community), the possibility for the interactor to disperse during the experiment, the similarity of generation for interaction and dispersal (same generation, or different generation, e.g. next generation for the effect of predation risk experienced by parents on offspring dispersal, or previous generation for the effect of nest predation risk on parent dispersal). Fifth, we added the type and characteristics of the study: experimental versus observational study, laboratory, semi-natural or field study, as well as the duration of the study in days.

In addition to the information extracted from the studies, we further searched within the literature for information on the focal species' generation time, the home range of the two interacting species [44–48] (unfortunately only found for 17 es), the level of generalism of the two interacting species (rated from 1 to 4 depending on whether they interact with only one

species, with species from the same genus or family, with species from the same order, or with species from different orders) and interaction strengths between pairs of species (electronic supplementary material, table S2). These interaction strengths between pairs of species found in the database are given as standardized effects of the presence or abundance of the interacting species on a fitness-related trait in the focal species (survival, fecundity, body condition, body growth or abundance), found either directly in the screened articles (166 es) or in a larger literature search (191 es; interaction strength was missing for 40 es). A single author (J.C.) searched for the strength of interaction and was different from the author calculating effect sizes for interaction effects on dispersal (E.B.) in order to reduce, without fully preventing, biases in the estimation of strength and its covariation with dispersal response. There was also a large variation in the experimental conditions of dispersal and fitness-related traits studies, which should result in a more conservative approach. As we were unable to extract generation time for two taxa, we imputed the median generation time of their closest taxa in the database.

We used taxonomy as a proxy for phylogenetic relatedness, using the *taxize* package v. 0.9.100 [49] to gather taxonomic information from the NCBI database. When the taxon considered was absent from the NCBI database, we used the GBIF (<https://www.gbif.org/>) or ITIS (<https://www.itis.gov/>) databases. We then calculated a taxonomic phylogenetic tree from the taxonomic data (kingdom–phylum–class–order–family–genus–species) and used Grafen's method of computing branch length [50] with the *ape* package v. 5.1-1 [51] (electronic supplementary material, figure S2).

(d) Statistical analyses

We studied the impact of interacting species on dispersal through multilevel mixed effects meta-analytic models via the *rma.mv* function of the *metafor* v. 4.2-0 package [52] in R v. 4.3. 1 [53]. We used a model selection approach to investigate our questions, thus the global model contains moderators for all questions of interest.

In the first step, we investigated whether the type of interactor (i.e. beneficial interactor (resource, host and mutualist) versus detrimental interactor (predator, competitor and parasite)) interacted with our moderators of interest to drive dispersal response to interacting species presence or abundance (figure 1). To do so, we ran a full model with:

- all pairwise interaction between the type of interactor (beneficial/detrimental) and the dispersal phase, the level of generalism of the focal species, the level of generalism of the interactor, the type of manipulation of the interacting species, the level of community complexity, the possibility for the interacting species to disperse, the similarity in the generation between the interaction and dispersal phase, the type of study (observational versus experimental), the centred log duration of the experiment and the centred log generation time of the focal species as moderators of interest and
- the study ID, the focal species ID, the focal species shared phylogenetic relatedness (branch length from the taxonomic phylogenetic tree) and the interacting species ID as random effects (see electronic supplementary material, Box S2 for the full model equation).

We then used the dredge function from the *MuMIn* v. 1.47.5 [54] package to select models with the best-fixed structure and averaged models within $\Delta AIC_c < 2$. We calculated the averaged conditional estimates from this model with the sum of weights of the metric across the models (SW, aka relative importance). We further refitted a model using all of the moderators present in the averaged best model to assess heterogeneity to confirm sources of variance across the dataset and computed the I^2 at each level, corresponding to the ratio of true heterogeneity to total observed variation. To understand whether there was publication bias, we visualized effect sizes using funnel plots of the residuals of this model and calculated Rosenberg's fail-safe number [55], which estimates the number of missing values averaging a z-value of zero needed to make effect sizes statistically insignificant. Third, we ran Egger's regressions [56] using the meta-analytic residuals as the response variable and the precision (defined as the square root of the inverse of variance) as the moderator. Intercepts of this regression that do not overlap zero are evidence of publication bias [57]. Finally, we analysed temporal trends in effect sizes that could indicate time-lag bias [57] by adding the interaction between time and the consequence of the interaction on fitness to the model containing all moderators present in the best model.

In a second step, we assessed the effects of moderators for beneficial and detrimental interactions separately because the effect sizes of their effects on dispersal are of opposite signs (i.e. beneficial interactions reduce dispersal propensity while detrimental interactions increase it). We divided the dataset into beneficial and detrimental interactors, and for each data subset, we fitted a full model with the same random effects as the above model and the exact nature of the interaction (i.e. resource, host and mutualist for the beneficial interactors subset and predator, parasite and competitor for the detrimental interactors subset), the dispersal phase, the level of generalism of the focal species, the level of generalism of the interactor, the type of manipulation of the interacting species, the level of community complexity, the possibility for the interacting species to disperse, the similarity in the generation between the interaction and dispersal phase, the type of study (observational versus experimental), the centred log duration of the experiment and the centred log generation time of the focal species as moderators of interest (electronic supplementary material, Box S2). We used the same model selection and model averaging procedure as above to select the best-averaged model. We further refitted models using all of the moderators present in the averaged best models to assess heterogeneity, study publication bias and finally plot results by the moderator. We used the *emmeans* package v.1.8.8 [58] to calculate the overall adjusted effects, as well as the estimated marginal means for different levels of each moderator.

Finally, because we were unable to gather home range and interaction strength information for most pairs of species, we ran two separate analyses for these two questions on the subset of studies for which we had information (7 studies with 17 effect sizes for home range, 108 studies with 357 effect sizes for interaction strength). Models used the study ID, focal species ID and

interactor ID as random effects and either the centred log ratio of home ranges between the focal species and the interactor or the interaction strength as a fixed moderator.

3. Results

(a) Summary of the dataset

We identified 118 studies that met our inclusion criteria, with 397 effect sizes for 144 focal species and 165 interacting species. Focal species spanned a wide range of taxa, with Arthropoda being the most represented (236 effect sizes), followed by Chordata (70) and Ciliophora (47), and then Nematoda, Mollusca, Annelida and Cryptophora (electronic supplementary material, figure S2, S3). As we restricted our search to actively dispersing species, plants were excluded. Our database further reflected a taxonomic bias in dispersal publications, with the number of effect sizes per taxonomic group significantly deviating from the frequencies expected from the diversity of species in the Catalogue of Life [59,60] through the recorded number of species in each group ($\chi^2 = 354$, d.f. = 4, $p < 2e^{-16}$; electronic supplementary material, table S3). Specifically, Chromista was overrepresented, and among Animalia, Arthropoda represented 68% of our effect sizes but was still underrepresented (83% under the null expectation) and Chordata was overrepresented (20% of observed effect sizes compared with 5% expected; electronic supplementary material, table S3). Such overrepresentation of Chordata is common in ecological studies, and the magnitude of overrepresentation is much lesser in our database than in behavioural studies where, for instance, Chordata represent up to 71% of publications [59]. The database included 152 effect sizes for interactions with beneficial interactors including resources (125), mutualists (21) and hosts (6), and 245 effect sizes for interactions with detrimental interactors including predators (116), competitors (73) and parasites (56). Studies also varied for the dispersal phase considered, with 275 considering emigration, 48 transience, and 74 monitoring the full dispersal process, as well as for the method used to manipulate the interacting species (actual presence or absence of interacting species, varying abundance, or cues of presence; see electronic supplementary material, figure S3, S4 and table S2 for a further exploration of the moderators).

(b) Description of the models and publication bias

We first studied how the type of interactor (beneficial versus detrimental interactor) and moderators affected the context-dependency of dispersal on species interactions using the full dataset. Our averaged best model included several pairwise interactions between the type of interactor (beneficial or detrimental) and the dispersal phase (emigration, transience or full dispersal), the type of study, the duration of the study and with other moderators having weaker effects (table 1). This model found important heterogeneity among studies ($I^2_{\text{study}} = 63.2\%$), as well as some heterogeneity related to the focal species' identity ($I^2_{\text{focal}} = 8.3\%$), phylogeny ($I^2_{\text{focal}} = 8.3\%$) and the interactor's identity ($I^2_{\text{interactor}} = 16.8\%$), for a total heterogeneity of $I^2 = 96.7\%$. Such high heterogeneity is expected in ecology and evolution meta-analyses, with the mean heterogeneity being 91.7% [61]. Funnel plots, Egger's test and the Rosenberg fail-safe number showed no significant publication bias: funnel plots did not reveal significant asymmetry (electronic supplementary material, figure S5), Egger's test showed an intercept that crossed zero for the residuals intercept ($[95\% \text{ CI}] = 0.13 [-0.03, 0.28]$, $t = 1.6$, d.f. = 395, $p = 0.119$) and the Rosenberg fail-safe number was very high ($n = 47\,929$). Additionally, we found that the effect size changed over time, suggesting a time-lag effect that was only present for beneficial interactors (electronic supplementary material, table S4).

In a second step, we split the dataset according to the previously defined beneficial and detrimental interactor types, replacing these broad types with the exact nature of the interaction (predators, parasites, competitors, resources, hosts or mutualists) as a moderator on the two data subsets. The two analyses did not retain the same moderators, suggesting that the importance of a moderator depended on the broad type of interaction (table 2; see the following text for description). Both models showed important heterogeneity ($I^2 = 93.9$ versus 95.5% respectively for beneficial versus detrimental interactions), but the distribution of the heterogeneity varied to a large extent among datasets, with a more important among-study effect for beneficial interactions ($I^2_{\text{study}} = 88.0$ versus 45.8%) and a larger importance of species identity and species phylogeny for detrimental interactions ($I^2_{\text{focal}} = 2.6$ versus 13.8% , $I^2_{\text{phylo}} = 2.6$ versus 13.8% and $I^2_{\text{interactor}} = 0.7$ versus 22.1%). When looking at the publication bias of those models with funnel plots and Egger's test, we found some asymmetry for the detrimental interaction dataset (electronic supplementary material, figure S6; Egger's test intercept $[95\% \text{ CI}] = 0.30 [0.11, 0.48]$, $t = 3.2$, d.f. = 243, $p = 0.002$, Rosenberg fail-safe $n = 30\,695$), suggesting some publication bias, but not for the beneficial interaction dataset (electronic supplementary material, figure S6, Egger's test intercept $[95\% \text{ CI}] = -0.21 [-0.64, 0.22]$, $t = -0.98$, d.f. = 150, $p = 0.33$, Rosenberg fail-safe $n = 17\,746$).

(c) Does the impact of interacting species on dispersal depend on the nature of species interactions?

Our global model found that the type of interactor and its interaction with various moderators affected the dispersal response to interacting species (table 1). Overall, the marginal effect size of this global model crossed zero ($-0.029 [-0.267, 0.209]$ adjusted effect $[95\% \text{ CI}]$), which was explained by the mix of decreasing and increasing effects on the dispersal of beneficial and detrimental interactions (table 1). When we divided the dataset into beneficial and detrimental interactors, dispersal propensity indeed decreased (adjusted effect: $-0.55 [-0.92, -0.17]$) and increased (adjusted effect: $0.33 [0.06, 0.59]$), respectively, when beneficial interactors and detrimental interactors were present or more abundant (figure 2a).

Table 1. Summary from the averaged best model investigating the effect of moderators on impacts of interacting species on focal species dispersal. The results issue from a model selection from a full model described in electronic supplementary material, box S2, averaging estimates from models where $\Delta AICc < 2$. The results show the conditional averaged estimates and s.e., z and p values, as well as the sum of weights of the moderator (SW). p -values < 0.05 are denoted in bold.

moderator	level	estimate	s.e.	z-value	p-value	SW
intercept		−0.36	0.19	1.94	0.053.	
dispersal phase	full dispersal	0.03	0.23	0.12	0.902	1.00
	transience	−1.30	0.36	3.64	<0.001***	1.00
centred log duration		−0.13	0.04	3.28	0.001**	1.00
centred level of generalism focal species		0.23	0.11	2.09	0.037*	1.00
type of community	simple community	0.89	0.24	3.69	<0.001***	1.00
	complex community	0.73	0.29	2.51	0.012*	1.00
type of interactor	beneficial	−0.29	0.20	1.46	0.145	1.00
type of study	observation	0.16	0.31	0.53	0.597	1.00
	beneficial:					
	full dispersal	0.58	0.36	1.61	0.107	1.00
type of interactor:	beneficial:					
dispersal phase	transience	1.39	0.42	3.27	0.001**	1.00
type of interactor:						
centred log duration	beneficial	0.23	0.06	3.83	<0.001***	1.00
type of interactor:	beneficial:					
type of study	observation	−1.44	0.52	2.75	0.006**	1.00
centred level of generalism interactor		−0.21	0.11	2.02	0.044*	0.92
type of manipulation of interactor	abundance	−0.14	0.11	1.33	0.185	0.69
	cues of presence	0.28	0.18	1.50	0.134	0.69
centred log generation time		0.06	0.04	1.28	0.200	0.31
type of interactor:						
centred log generation time	beneficial	−0.09	0.06	1.60	0.109	0.20
similarity generation dispersal interaction	different generation	0.26	0.29	0.90	0.369	0.17
type of interactor:						
centred level of generalism focal species	beneficial	0.12	0.17	0.67	0.505	0.08

The exact nature of the beneficial interactor (i.e. resources, hosts or mutualist) had an important effect on dispersal propensity (SW = 0.83), while the nature of the detrimental interactor (i.e. predators, parasites or competitors) had only weak effects (SW = 0.15, [table 2](#)). While beneficial interactions generally reduced dispersal propensity, parasites tended to increase their dispersal propensity when their host was present or more abundant ([table 2](#), electronic supplementary material, table S5, [figure 2b](#)). On the contrary, all detrimental interactions had similar effects on dispersal, with competitors tending to have a stronger effect ([table 2](#), electronic supplementary material, table S5, [figure 2b](#)).

(d) Does the dispersal response depend on the spatio-temporal dynamics of interacting species?

Moderators related to spatio-temporal dynamics influenced the strength of interaction-dependent dispersal. In the full dataset, the interactions between the type of interactors and the dispersal phase had a strong impact on dispersal (SW = 1, [table 1](#)). This was confirmed with data subsets on beneficial and detrimental interactors (SW ≥ 0.91 , [table 2](#)). The presence or abundance of detrimental interactors increased the rates of emigration and full dispersal while it decreased dispersal distance (i.e. transience phase, [figure 3](#), electronic supplementary material, table S5). Beneficial interactions had a stronger negative effect on dispersal propensity at the emigration phase than for the transience phase and the full dispersal process ([figure 3](#), electronic supplementary material, table S5).

In addition, longer experiments showed weaker effects of interactions on dispersal and this attenuation was stronger for detrimental than for beneficial interactions ([tables 1 and 2](#), SW = 1 versus 0.74, respectively, electronic supplementary material, figure S7). The generation time of the focal species further had a very weak effect for detrimental interactions only, with a slightly stronger positive effect of detrimental interactors on dispersal for species with longer generation times (SW = 0.24, [table 2](#), electronic supplementary material, figure S7).

We found that increasing ratios of home ranges between the focal species and the interactor tended to decrease the positive effect of detrimental interactors on dispersal, although the effects are to be taken with caution owing to the very low sample size (only seven studies on detrimental interactions with 17 effect sizes, see §2 and electronic supplementary material, table S6).

Table 2. Summary from the averaged best model investigating the effect of moderators on impacts of interacting species on focal species dispersal subsetting the data by type of interactor. The results are issued from a model selection from a full model, averaging estimates from models where $\Delta AICc < 2$. The results show the conditional averaged estimates and s.e., z and p values, as well as the sum of weights of the moderator (SW). p-values < 0.05 are denoted in bold.

data subset	moderator	level	estimate	s.e.	z-value	p-value	SW
detrimental	intercept		-0.12	0.24	0.51	0.610	
		full dispersal	0.06	0.22	0.28	0.780	1.00
	dispersal phase	transience	-1.18	0.34	3.49	<0.001***	1.00
	centred log duration		-0.12	0.04	2.77	0.006**	1.00
		abundance	-0.17	0.13	1.29	0.196	1.00
	type of manipulation of interactor	cues of presence	0.58	0.25	2.36	0.018*	1.00
		simple community	0.54	0.26	2.12	0.034*	0.78
	level of community complexity	complex community	0.69	0.28	2.43	0.015*	0.78
	centred level generalism focal		0.27	0.16	1.71	0.087.	0.70
	centred level generalism interactor		-0.17	0.11	1.47	0.143	0.39
	type of study	observation	0.42	0.30	1.40	0.161	0.25
	centred log generation time		0.06	0.04	1.30	0.194	0.24
	possibility for interactor to disperse	yes	0.31	0.28	1.13	0.256	0.21
	similarity in generations between dispersal and interaction	different generation	0.54	0.38	1.43	0.154	0.20
		competitor	0.76	0.37	2.04	0.041*	0.15
beneficial	intercept		-0.71	0.22	3.29	<0.001***	
		full dispersal	0.45	0.18	2.47	0.013*	0.91
	dispersal phase	transience	0.08	0.24	0.34	0.733	0.91
		host	1.73	0.70	2.48	0.013*	0.83
	nature of interactor	mutualist	0.51	0.82	0.62	0.537	0.83
	centred level generalism interactor		-0.46	0.26	1.80	0.072.	0.79
	centred log duration		0.06	0.04	1.60	0.110	0.74
	type of study	observation	-0.60	0.42	1.40	0.161	0.21
	centred level generalism focal		0.13	0.14	0.94	0.345	0.10

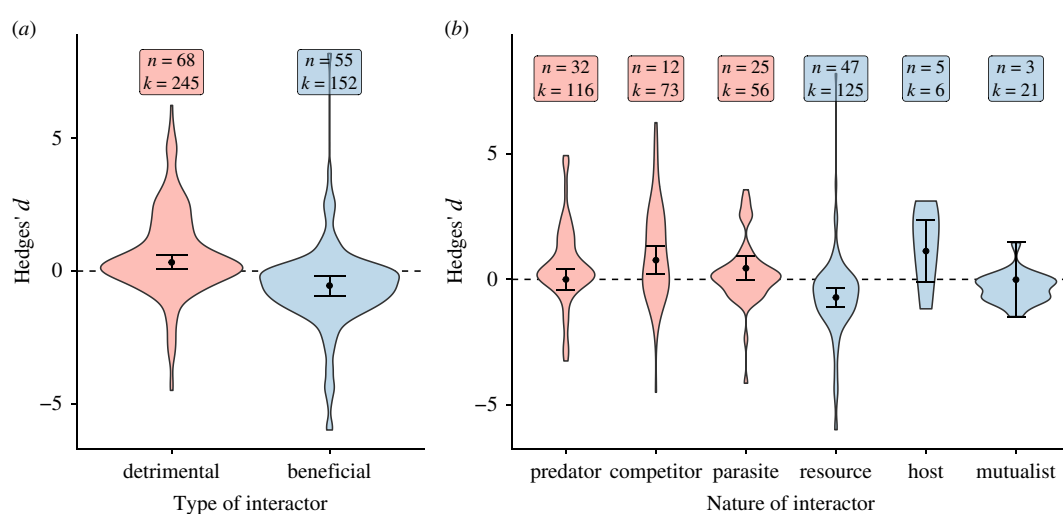


Figure 2. The effect of interacting species on dispersal of the focal species depends on the type of interactor. Effect of (a) the type of interactor (red: detrimental interactors, blue: beneficial interactors) and (b) the nature of interactor (predator, competitor, parasite, resource, host and mutualist) on the effect of interacting species on dispersal (positive Hedges' d values: increased dispersal in the presence of interactors, negative: decreased dispersal). Violin plots of raw effect sizes, with points and error bars corresponding to the marginal effect means and 95% CI from the two meta-analytic models for the subsets (i.e. beneficial and detrimental interactions; table 2, electronic supplementary material, table S5) and labels corresponding to the number of studies across moderators n and the number of effect sizes across categorical moderators k .

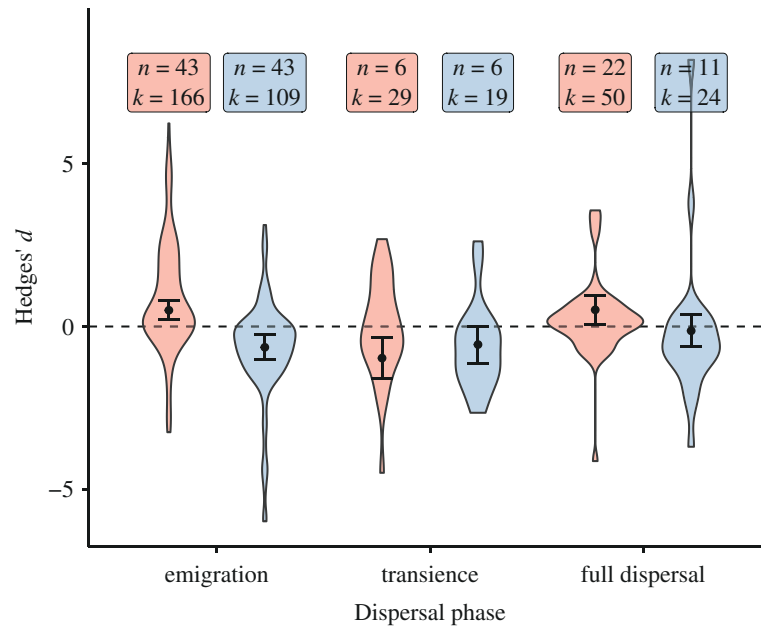


Figure 3. The effect of interactors on focal species dispersal varies depending on the dispersal phase considered. Effect of the dispersal phase and the type of interactor (red: detrimental interactors, i.e. predators, competitors, parasites, blue: beneficial interactors, i.e. resources, hosts, mutualists) on the effect of interacting species on dispersal (positive Hedges' d values: increased dispersal in the presence of interactors, negative: decreased dispersal). Violin plots of raw effect sizes, with point and error bars corresponding to the marginal effect means and 95% CI from the two meta-analytic models for the subsets (i.e. beneficial and detrimental interactions, table 2, electronic supplementary material, table S5), and labels corresponding to the number of effect sizes across categorical moderators k and the number of studies across moderators n .

(e) Do the interaction strength and ecological complexity affect the dispersal response?

Moderators related to the perception of interaction strength by an individual and the ecological complexity influenced the strength of interaction-dependent dispersal. The full database showed a marked importance of the community complexity level ($SW = 1$) and a weaker importance of the way the interactor was manipulated ($SW = 0.69$, table 1). Subsetting by interactor types showed that these effects were mainly found for detrimental interactions ($SW = 1$ and 0.78 , respectively, for community complexity level and type of manipulation, table 2). More complex systems with three or more species or natural communities showed stronger positive effects (figure 4, electronic supplementary material, table S5), while manipulation of cues of presence showed stronger positive effects than manipulation of presence (figure 4, electronic supplementary material, table S5). Whether the study was experimental or observational was unlikely to have an effect ($SW \leq 0.25$, table 2).

The level of generalism of both species was evidenced as important ($SW \geq 0.92$, table 1). Subsetting beneficial and detrimental interactions showed that higher levels of generalism of the focal species led to slightly stronger positive effect of detrimental interactions on dispersal ($SW = 0.70$, table 2, figure 5, electronic supplementary material, table S5) and more generalist beneficial interactors had slightly stronger negative effects on dispersal ($SW = 0.79$, table 2, figure 5, electronic supplementary material, table S5).

The possibility for the interactor to disperse and the similarity of generation between interaction and dispersal were unlikely to have a strong effect on context-dependent dispersal ($SW \leq 0.21$, table 2, electronic supplementary material, table S5).

We further gathered a continuous estimate of interaction strengths between pairs of species present in our database from the literature (193 pairs of species and 357 effect sizes). We found a strong negative relationship between measured interaction strength and dispersal response to interaction (electronic supplementary material, table S7, figure 6). While matching the effect of the binary interaction type (see above), this continuous interaction strength was a better predictor (electronic supplementary material, table S7, figure 6). When restricting this analysis to studies measuring concomitantly the dispersal response to interaction and the interaction strength (166 effect sizes), the impact of interaction strength was an even better predictor (electronic supplementary material, table S7, figure 6).

4. Discussion

Species do not move randomly among habitats in a landscape [62]. On the contrary, a number of external cues about abiotic and biotic contexts, and internal cues about physiological states influence individuals' decisions to leave their habitats, to orient themselves in a landscape and to settle in a novel habitat [4]. Context-dependent dispersal is now well-supported by accumulating empirical evidence and theoretically bolstered by adaptive dispersal theory [5,7,13,19,63–67]. Accordingly, individuals should leave habitats with adverse conditions and search for better ones, as long as the energy, time and risk barriers to dispersal (i.e. dispersal costs) do not offset the benefit [22]. Using a systematic review approach, we investigated the relationship between species interactions—a key driver of dispersal suffering from an absence of global synthesis in the

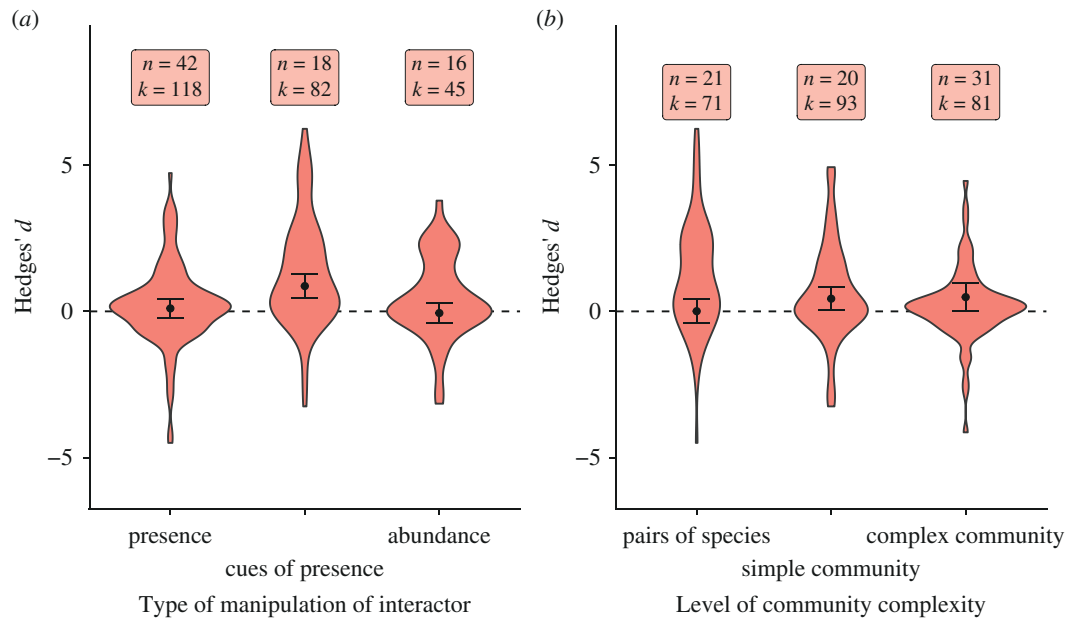


Figure 4. For detrimental interactions, the effect of interacting species on focal species dispersal varies depending on the biotic context. Effect of (a) the type of manipulation of the interactor (i.e. presence, cues of presence or abundance) and (b) the level of community complexity (pairs of species, simple community, complex community) on the effect of detrimental interactors on dispersal (positive Hedges' d values: increased dispersal in the presence of interactors, negative: decreased dispersal). Violin plots of raw effect sizes, with point and error bars corresponding to the marginal effect means and 95% CI from the meta-analytic model for the detrimental interactors data subset (table 2, electronic supplementary material, table S5), and labels corresponding to the number of effect sizes across categorical moderators k and the number of studies across moderators n .

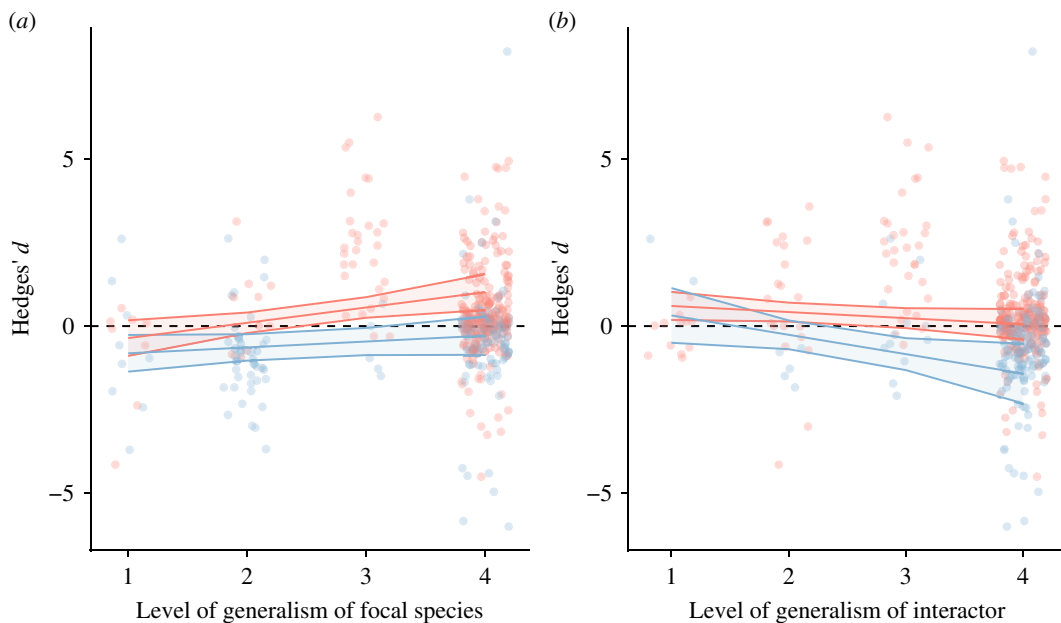


Figure 5. The effect of interactors on focal species dispersal varies depending on both species' level of generalism. Effect of the generalism of (a) the focal species or (b) the interactor and type of interactor (red: detrimental, blue: beneficial) on the effect of interacting species on dispersal (positive Hedges' d values: increased dispersal in the presence of interactors, negative: decreased dispersal). The level of generalism is rated from 1 to 4 on whether species interact only with one species (1), with species from the same genus or family (2), with species from the same order (3), or with species from different orders (4). Points represent the effect sizes, and lines and confidence intervals are displayed from marginal means and 95 % CI from the two meta-analytic models calculated at the four levels of generalism.

literature—and dispersal plasticity including all types of species interactions, across diverse taxonomic groups, focusing on actively dispersing organisms.

Our first main result is that the interaction-dependence of dispersal matches the expected fitness consequences of the interaction. The presence or abundance of detrimental interactors (consumers, parasites or competitors) increased the dispersal propensity of a focal species. Conversely, the presence or abundance of beneficial interactors like resources, hosts and mutualists decreased the dispersal propensity of a focal species. While clearly fitting basic adaptive dispersal theory, there is a large variation around this general pattern that is explained by dependencies on the dispersal phase studied. We found that the impacts of detrimental interactions changed from positive to negative depending on whether the study focused on the emigration or transience phase, and we found that the dependencies on the duration of the experiment, on the complexity

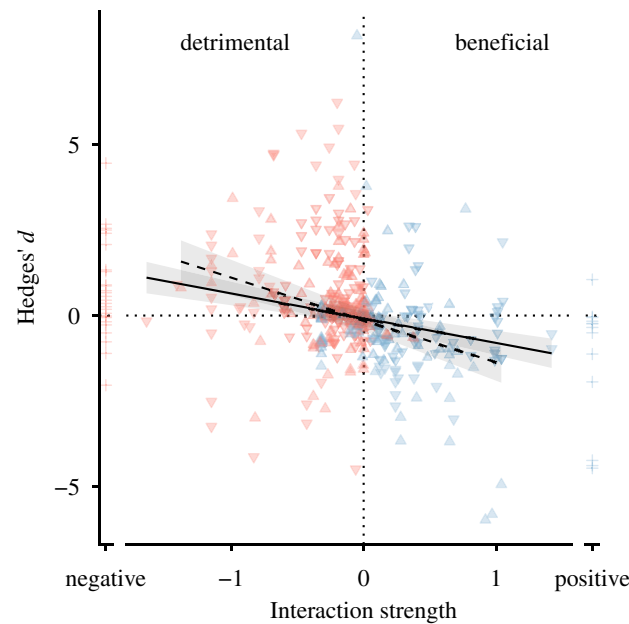


Figure 6. The effect of interactors on focal species dispersal varies on the strength of interaction between species. Effect of the interaction strength between pair of species and type of interactor (red: detrimental, blue: beneficial) on the effect of interacting species on dispersal (positive Hedges' d values: increased dispersal in the presence of interactors, negative: decreased dispersal), for the 357 effect sizes for which we could retrieve interaction strength. Coloured points represent interaction strength as a function of Hedges' d , for either the subset of data for which interaction strength was measured concomitantly to dispersal ('strict database', triangles, 166 es), for which the interaction strength was found in the secondary literature (upside-down triangles, 191 es), or for which the interaction strength was not found at all and thus is only categorized as positive or negative (crosses, 40 es). Lines and ribbons represent the effect of interaction strength on dispersal from the meta-analytic model, either on the strict database (dashed line, electronic supplementary material, table S7), or on all measures of interaction strength (full line, electronic supplementary material, table S7).

of the community studied and on other moderators related to ecological complexity, interaction strength and spatio-temporal dynamics.

We expected the context-dependency of dispersal to depend on the exact nature of the interaction, with responses to predators, for example, not being the same as responses to parasites owing to differences in the efficiency of dispersal in mitigating these detrimental interactions (see §1). This last result was only partially supported, with only weak differences between species responses to predators, parasites and competitors for detrimental interactions and a difference between responses to hosts and resources for beneficial interactions. This weak variation is likely not explained by a potential scarcity of studies involving predators because the sample size per interaction is relatively high (32 studies and 117 effect sizes), competitors (12 studies and 73 es) and parasites (25 studies and 56 es). Similarly, the difference between responses to host and resource presence was unexpected, although the sample size for hosts was very low. Consumers logically decreased their dispersal propensity away from places with available resources, while parasites tended to disperse away from habitats with more hosts. We posit that this surprising result may be explained by underlying positive effects of host occurrence on the population growth and dynamics of parasites leading to intertwined effects of inter- and intraspecific interactions. However, the number of studies investigating both inter- and intraspecific interactions and the population growth of interacting species was too limited [68] to test this hypothesis.

Similar to the reported effects of intraspecific density [19], we showed that the consequence of interspecific interactors' presence and abundance led to complex responses on dispersal. Species have been shown to respond to intraspecific density through emigration in diverse ways, with 30% of the 145 studies reviewed showing no density-dependent dispersal, 36% showing positive density-dependent dispersal and 25% negative density-dependent dispersal, with 9% representing nonlinear responses [19]. Our meta-analysis similarly showed important heterogeneity in dispersal responses to interspecific interactions, which is not surprising given the dependency of interaction strength itself on biotic and abiotic context [49]. The strength of biotic interactions was shown to vary particularly along abiotic gradients, with spatial and temporal gradients showing lower variation, and also to vary particularly in laboratory studies, while mesocosm and field studies showed lower variation [49]. Chamberlain *et al.* [49] even reported changes in the signs of the interaction across contexts within a study, with an important proportion of changes among mutualists and competitors. It is thus possible that context-dependent variation in the strength of biotic interactions, owing to experimental design, abiotic or biotic variation, would in return lead to variation in the context-dependency of dispersal. Overall, our literature search did not yield many examples of variation in the effect of heterospecifics on dispersal with other abiotic and biotic contexts (but see some studies on the interplay between intraspecific and interspecific conditions [69–74], between habitat quality and predation risk [75,76], between abiotic conditions (e.g. sunshine, temperature) and diverse biotic conditions [77,78]). The interplay between biotic and abiotic environmental dimensions, phenotype and dispersal can further make the relationship between interspecific interactions and dispersal complicated [68]. Dispersal is indeed a multi-causal process [79], responding to multiple internal and external cues that are themselves intertwined. For example, species interactions strongly influence the density of interacting species. Predation, by decreasing prey density, would

thereby decrease intraspecific competition [6] and potentially increase inbreeding. On the other hand, the response to intraspecific competition itself can vary with predation risk, as is the case in *Notonecta undulata* where the intraspecific density threshold for dispersal was shifted downwards when fish predator cues were present [69]. The effect of predation risk can further depend on the structure of the habitat, such as in hydropsychid larvae where the use of drift dispersal to avoid predators was favoured in structurally simple habitats, while habitats with a dense periphyton mat allowed sufficient microhabitat refugia from predators to decrease dispersal [75]. The resulting dispersal responses to this blend of central dispersal drivers are difficult to predict. Interestingly, studies manipulating only detrimental interaction cues led to a greater positive impact on the focal species' dispersal than those examining the actual presence of interacting species. Such stronger effects of cues can be related to the notion of a landscape of fear [26,80], where the mere presence of predators can have stronger impacts than actual prey consumption. The type of cues affecting the dispersal response can vary depending on the species and their specific biology, such as on *Baetis thermicus* larvae where larvae detected the risk of predation by diurnal foragers such as salmon (*Oncorhynchus masou*) mainly through visual cues, increasing drift rate, while predation of the nocturnal sculpin (*Cottus nozawae*) was mainly detected through chemical cues [81].

The actual interaction strength between species, perceived within the actual study conditions, should therefore better predict the effect of the interactor's presence on dispersal [14]. However, only 43% of studies quantified the interaction strength along with dispersal responses, and thus we used indirect measures of interaction strength through the generalism of interacting partners towards each other (e.g. single or multiple predator species for a focal prey species). We found that the level of generalism of interacting species affected the dispersal outcome. Counterintuitively, the level of generalism of the focal species was mainly important for detrimental interactions, where positive effects of interactor presence on dispersal were strongest for more generalist focal species, while the level of generalism of the interacting species was more important for beneficial interactions, with a stronger negative impact for more generalist interactors. We were expecting the level of interactor generalism to be of greater importance for detrimental interactors, as for example, prey might have a higher motivation to escape highly specialized predators than generalist predators. Furthermore, we were expecting that more specialized focal species may pose a broader burden on their resource, increasing demographic fluctuations and thus the extinction probability of the focal species, leading to a stronger effect on dispersal [17].

We further screened articles and the broader literature to gather information about interaction strength between pairs of species, resulting in variation in the populations or study condition used (densities and type of species manipulation) in the studies on dispersal and interaction strength, a potential source of discrepancies [49]. Furthermore, the interaction strength was measured through fitness-related traits that varied among pairs of interacting species (i.e. survival, fecundity, body condition and abundance). While this result should be taken with caution and although the approach should be conservative, the estimated strength of interactions between species predicted the dispersal responses to interaction well, and even better than using the binary beneficial/detrimental type of interaction (electronic supplementary material, table S7). When restricting our dataset to studies jointly measuring the dispersal response and interaction strength, we even better estimated the effect of interaction strength on dispersal. These results demonstrate the importance of assessing interaction strengths and fitness consequences concomitantly with dispersal dependencies, in single and multiple conditions, to better understand interaction-dependent dispersal and why it varies among species, interaction types and ecosystems (figure 1).

Our results further showed that the effects of interactors varied with the dispersal phase studied. Detrimental interactions had stronger positive impacts on emigration than on full dispersal and even had negative impacts on transience. We expected predators, parasites and competitors to increase the dispersal of the focal species to avoid the potential negative consequences for fitness, and this was the case for emigration and full dispersal [15,82]. However, transience is a particularly vulnerable stage, where the risk of predation may be heightened; thus, a decrease in dispersal distance, for instance, may be expected. Similarly, hosts may increase their dispersal behaviour to escape an infested habitat [15] and parasites themselves can manipulate their hosts' dispersal to increase contact rate and the transmission of parasites [21]. However, by diverting their resources, parasites can constrain their hosts' ability to move [21]. Such contrasted effects of parasitism can be illustrated by a study on *Notonecta*, where parasite infection reduced *Notonecta* dispersal ability but parasitism risk increased dispersal distance [83]. We thus expected factors influencing emigration decisions and dispersal distance to be fundamentally different, with emigration decisions varying solely with local conditions and dispersal distance varying with the ability to disperse and the spatial scale of the interaction. The impact of beneficial interactions also depended on the dispersal phase studied, with strong negative impacts on emigration, slightly weaker impacts on transience and no effect on full dispersal. The difference between the effects of beneficial and detrimental interactors might reflect a dependency on both the local and the broader spatial context for detrimental interactors, while the local context was the main driver of dispersal decisions for beneficial interactors. Again, a more precise estimate of the scale and decay of interaction strength through the landscape and its effects on focal species fitness at each dispersal phase may help resolve this question. The information we could gather on species home ranges was fairly limited, but we found that the ratio of home ranges influenced the focal species dispersal, with a tendency for larger home ranges for focal species relative to the interactor decreasing the dependency of dispersal on detrimental interactions. This larger home range may allow focal species to escape detrimental interactors through changes in spatial distribution within their habitat, a likely less costly strategy than dispersing away. The interplay between species interaction and dispersal at different spatial scales should play an important role in metacommunity dynamics. Indeed, a recent theoretical study has shown that the spatial scales of dispersal and species interactions have opposite effects on ecosystem functioning [84]. A modelling effort illustrating the impacts of context-dependent dispersal in simple three-level food chain communities shows that simultaneous resource- and predator-dependent emigration reduced local fluctuations of population dynamics through time, and increased metacommunity stability [13]. In competitive communities of two *Callosobruchus* species, subdivision of the habitat into patches within a metacommunity structure allows for new niche-differentiating mechanisms through a dispersal–competition trade-off

allowing species coexistence [85]. Further, the dependency of dispersal on spatial scale should itself depend on the spatio-temporal autocorrelation of population dynamics between interacting species across scales [6,13,18], potentially leading to the co-evolution of dispersal of interacting species [17].

We were also expecting the impact of the interacting species to depend on the larger biotic context. Specifically, we expected that more complex communities could lead to a 'dilution effect' where the cues and the impact of each interacting species on the focal species' dispersal may be weaker when diluted in a larger number of species interactions. We observed the opposite effect, with stronger positive effects of detrimental interactors being observed in more complex communities than for studies on pairs of interacting species. This could be explained by methodological differences between studies on pairs of interacting species, which are very often laboratory studies, and studies on more complex communities, often corresponding to field studies or semi-natural mesocosm studies. Oversimplified set-ups may actually buffer the effects of interaction on dispersal through acclimation to threats and an overall lower perception of risk. Because of the inherent nestedness of community complexity and experimental set-up, we were not able to put both moderators in the models. An alternative explanation rests on a confounded effect of multiple species interactions. As mentioned above, field studies often lead to difficulties in disentangling effects on survival from effects on dispersal and in properly isolating the effect of a single species. For example, the abundances of a prey species and its different predator species are often correlated, leading to difficulties in isolating the effect of each predator species without intensive monitoring of all species at play [86]. The same reasoning can be made for other interacting species like resources for consumers, as in flying squirrels (*Sciurus vulgaris*), which depend on multiple resources (spruce, birch and alder catkin) that likely covary and can alternatively appear as the main driver of fitness [87,88], potentially hampering the estimate of their respective effects on dispersal.

Finally, we showed that the duration of the study modulates the effects of interactions on the dispersal of focal species. The longer the study lasted the closer the effect sizes were to zero for detrimental interactions, and to a lower extent for beneficial interactions. This effect may reflect an acclimation to the interacting species in experimental studies, reducing the sensitivity of individuals to stressful interactions and therefore their dispersal propensity to avoid them. In addition, not all individuals are equally likely to disperse [4] and/or to respond through dispersal to adverse abiotic and biotic conditions [64,89]. Shorter experiments may capture the most responsive individuals and the longer the study lasts the weaker the overall response should be. However, one can alternatively argue that less responsive individuals would also react and disperse only after long-lasting experiments. Unfortunately, dispersal studies are often limited in time or space and might therefore misestimate the effect of interaction-dependent dispersal at the whole population scale.

Our systematic literature review focused only on actively dispersing species, and thus excluded passively dispersed taxa such as plants. It yielded a majority of articles on insects, with other groups like spiders, birds, nematodes, mammals or protists being less represented. While our dataset was taxonomically biased, it matched the taxonomic coverage of the systematic review on intraspecific density [19] and showed much lesser taxonomic bias than behavioural studies, for instance [59]. This highlights the importance of covering a wide range of taxa across the phylogenetic tree in dispersal studies to account for the diversity of dispersal behaviours and species interactions. Another knowledge gap highlighted by our literature search is the relative lack of studies on the interplay between species interaction and dispersal syndromes (but refer to [90–94] in our reference list). Given the suggested role of dispersal syndromes in fitness-dispersal relationships and eco-evolutionary dynamics of metacommunities [64,89], we would suggest that research groups integrate a more detailed characterization of the phenotype and its relationship to dispersal into their studies. Furthermore, a meta-analysis focusing on passively dispersing species would help to understand whether processes influencing interaction-dependent dispersal are similar to those affecting active dispersers. Finally, we want to highlight the following conclusions and ideas to stimulate further research on dispersal and species interaction:

— Methodological issues:

- (i) The *experimental set-up* matters. Oversimplified set-ups may buffer the effects of interactions on dispersal through acclimation to threats. On the other hand, field studies often prevent disentangling effects of biotic conditions on survival and dispersal. Further, they can struggle to isolate properly the effect of each species interaction on the dispersal of a focal species because interactions among different interacting species (e.g. interaction of a prey species with multiple predator species) often covary in time or space. Those issues are at the core of discussions on experimental versus observational approaches. Large-scale experiments that are monitored over time in more realistic ecological conditions as well as a more holistic investigation of biotic and abiotic drivers in the field might improve our understanding of the relationship between dispersal and species interactions.
- (ii) The duration of the experiment greatly influences the estimated relationship between dispersal and species interaction. This does not mean that we should run shorter experiments to increase the likelihood of finding larger effects because species interactions and dispersal phases last longer in nature than in an experiment. However, we should consider the temporal aspect as an additional factor when running an experiment manipulating species interactions on varying time windows and select appropriate durations relative to species' generation time. In addition, natural contexts often imply the *integration of cues* on interacting species *over a larger temporal window* within and between generations, thereby providing a more realistic estimate of information acquisition in stable and predictable environments and a poor estimate of enduring species interaction in changing environments.
- (iii) *Cues* might lead to stronger effects than the *actual presence* of an interacting species. A potential explanation to consider is that the actual presence often mixes direct effects of the interaction, including its numerical effects (i.e. predators consume prey), and species behavioural responses. For example, prey may intend to respond to cues about predation risk by leaving its habitat, but this intent might be repressed by the immediate lethal costs of doing so when actual predators are present. Such impacts of cues can be related to the landscape of fear, whereby predators have a disproportionately strong

effect on prey redistribution over the landscape compared to their direct consumptive effect [26,80]. This landscape of fear effect also implies that measuring interaction strength through fitness effects alone might underestimate its ecological impact mediated by behaviour.

— Ecological aspects of interaction-dependent dispersal

- (i) The numerical effects of species interactions further influence *intraspecific competition* through changes in population density. This main driver likely influences species fitness and dispersal propensity in an opposite direction to species interactions. Beneficial interactions likely increase population density while detrimental interactions decrease it [6]. The resulting consequence for dispersal calls for study designs testing the respective and interactive effects in a fully crossed manner [68].
- (ii) A clear pattern is the effects of *dispersal phase*. It has been pointed out repeatedly [4,5] that aside from our naive expectation that emigration and immigration decisions should mirror each other, the risks and benefits of species interaction likely vary between initial habitat, environments crossed during transience and new habitats to settle in. It appears important to investigate the fitness and dispersal consequences of species interactions through the three movement phases. A further review should focus on the consequences of interspecific interactions at the colonization stage.
- (iii) We need to improve our understanding of the *spatio-temporal dynamics* of interacting species. Indeed, an individual's decision to disperse from its current or natal habitat has large and lasting consequences for its life history [95]. Therefore, alternative responses to a threat might be favoured when the population dynamics of interacting species give room to those alternatives (e.g. asynchrony in predator and prey population dynamics). Modelling studies have shown the importance of spatio-temporal autocorrelation for dispersal dynamics [6,13,18].
- (iv) The dispersal response depends on the *interaction strength*. We have shown that beneficial and detrimental interactions lead to opposite dispersal responses, but the effect can be modulated by the type of interaction, the level of specialization between interactors and the dilution of the interaction by community diversity. More studies should aim at characterizing this interaction strength, from the local community level to higher spatial scales in a metacommunity context, to better understand its impacts on dispersal.

— Ecological and evolutionary consequences for metacommunities

- (i) *Moving from pairs of species to complex metacommunities* may be a difficult task. We have shown that the importance of context-dependent dispersal depends on the overall community context, thus experiments with pairwise interactions may fail to capture the complexity of the dispersal response and studies in natural communities may fail to tease apart the respective and interactive effects of multiple interactions. Nevertheless, modelling studies show that with even simple three-level communities, context-dependent dispersal between pairs of species has a strong impact on metacommunity dynamics [13].
- (ii) Context-dependent dispersal should shape metacommunity dynamics. When studying the consequences of dispersal at the landscape level, studies often treat dispersal as a constitutive trait of species and/or landscape features [84]. Our results evidence a dispersal plasticity in response to biotic interactions, particularly in the context of the landscape of fear [26,80], which should influence the species distribution and their match to local ecological conditions within a landscape.
- (iii) We need to better understand how *evolving landscapes can affect the context-dependency of dispersal*. Eco-evolutionary dynamics of species interactions should influence the evolution of both context-independent [17] and context-dependent dispersal [6,64], and conversely the eco-evolutionary dynamics of dispersal should influence species interactions and metacommunity dynamics [64]. These two evidenced assertions hamper the accurate predictions of metacommunity dynamics in a greatly and rapidly changing world.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and code are available at Zenodo: <http://dx.doi.org/10.5281/zenodo.10940162>. For review purposes, the data and code are attached as a zipped electronic supplementary material [96].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. E.B.: conceptualization, data curation, formal analysis, investigation, methodology, writing – original draft, writing – review & editing; D.L.: data curation, methodology, writing – review & editing; C.B.B.: data curation, writing – review & editing; D.B.: data curation, writing – review & editing; A.C.: data curation, writing – review & editing; M.D.: data curation, writing – review & editing; M.d.M.D.: writing – review & editing; J.D.: data curation; A.D.: data curation, writing – review & editing; E.A.F.: data curation, writing – review & editing; I.G.: data curation, writing – review & editing; S.J.: data curation, writing – review & editing; O.K.: data curation, writing – review & editing; F.M.: data curation, writing – review & editing; E.M.: data curation, writing – review & editing; T.P.: data curation, writing – review & editing; C.S.: data curation, writing – review & editing; N.S.: data curation, writing – review & editing; G.Z.: data curation, writing – review & editing; J.C.: conceptualization, data curation, methodology, validation, writing – original draft, writing – review & editing

Conflict of interest declaration. We declare we have no competing interests.

Funding. The idea of the study originated from a workshop on dispersal led by E.A.F. supported by a grant from the Agence Nationale de la Recherche (No.: ANR-19-CE02-0015) to E.A.F. We thank all participants of the workshop for fruitful discussions. This work was supported by LABEX TULIP (ANR-10-LABX-0041) and the EVENET network. This is publication ISEM-2024-125 of the Institut des Sciences de l'Evolution - Montpellier. J.C. was supported by a funding from the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme (grant agreement No 817779), M.d.M.D. was supported by Ayudas de Incorporación Científico Titular' (#2022301042; CSIC), O.K. was supported by a grant from the Agence Nationale de la Recherche (ANR-20-CE02-0023-01).

References

- Leibold MA *et al.* 2004 The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* **7**, 601–613. (doi:10.1111/j.1461-0248.2004.00608.x)
- Baguette M, Blanchet S, Legrand D, Stevens VM, Turlure C. 2013 Individual dispersal, landscape connectivity and ecological networks. *Biol. Rev.* **88**, 310–326. (doi:10.1111/brv.12000)
- Kubisch A, Holt RD, Poethke HJ, Fronhofer EA. 2014 Where am I and why? Synthesizing range biology and the eco-evolutionary dynamics of dispersal. *Oikos* **123**, 5–22. (doi:10.1111/j.1600-0706.2013.00706.x)
- Clobert J, Le Galliard J-F, Cote J, Meylan S, Massot M. 2009 Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12**, 197–209. (doi:10.1111/j.1461-0248.2008.01267.x)
- Bowler DE, Benton TG. 2005 Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev.* **80**, 205–225. (doi:10.1017/s1464793104006645)
- Poethke HJ, Weisser WW, Hovestadt T. 2010 Predator-induced dispersal and the evolution of conditional dispersal in correlated environments. *Am. Nat.* **175**, 577–586. (doi:10.1086/651595)
- Armstrong PR, Roughgarden JE, Losos EJB, Perrin AEN. 2005 The impact of directed versus random movement on population dynamics and biodiversity patterns. *Am. Nat.* **165**, 449–465. (doi:10.1086/428595)
- McPeck MA, Holt RD. 1992 The evolution of dispersal in spatially and temporally varying environments. *Am. Nat.* **140**, 1010–1027. (doi:10.1086/285453)
- Bocedi G, Heinonen J, Travis JMJ, Berger AEU, Bronstein EJJ. 2012 Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. *Am. Nat.* **179**, 606–620. (doi:10.1086/665004)
- Poethke HJ, Pfennig B, Hovestadt T. 2007 The relative contribution of individual and kin selection to the evolution of density-dependent dispersal rates. *Evol. Ecol. Res.* **9**, 41–50.
- Gros A, Poethke HJ, Hovestadt T. 2006 Evolution of local adaptations in dispersal strategies. *Oikos* **114**, 544–552. (doi:10.1111/j.2006.0030-1299.14909.x)
- Jacob S, Bestion E, Legrand D, Clobert J, Cote J. 2015 Habitat matching and spatial heterogeneity of phenotypes: implications for metapopulation and metacommunity functioning. *Evol. Ecol.* **29**, 851–871. (doi:10.1007/s10682-015-9776-5)
- Fronhofer EA *et al.* 2018 Bottom-up and top-down control of dispersal across major organismal groups. *Nat. Ecol. Evol.* **2**, 1859–1863. (doi:10.1038/s41559-018-0686-0)
- Fronhofer EA, Klecka J, Melián CJ, Altermatt F. 2015 Condition-dependent movement and dispersal in experimental metacommunities. *Ecol. Lett.* **18**, 954–963. (doi:10.1111/ele.12475)
- Boulinier T, McCoy KD, Sorci G. 2001 Dispersal and Parasitism. In *Dispersal* (eds J Clobert, E Danchin, AA Dhondt, JD Nichols), pp. 169–179. Oxford, UK: Oxford Academic. (doi:10.1093/oso/9780198506607.003.0013)
- de Casas RR, Willis CG, Donohue K. 2012 Plant dispersal phenotypes: a seed perspective of maternal habitat selection. In *Dispersal ecology and evolution* (eds J Clobert, M Baguette, TG Benton, JM Bullock), pp. 171–185. Oxford, UK: Oxford University Press. (doi:10.1093/acprof:oso/9780199608898.003.0014)
- Zilio G, Deshpande JN, Duncan AB, Fronhofer EA, Kaltz O. 2024 Dispersal evolution and ECO-evolutionary Dynamics in antagonistic species interactions. *Trends Ecol. Evol.* (doi:10.1016/j.tree.2024.03.006)
- Deshpande JN, Kaltz O, Fronhofer EA. 2021 Host–parasite dynamics set the ecological theatre for the evolution of state- and context-dependent dispersal in hosts. *Oikos* **130**, 121–132. (doi:10.1111/oik.07512)
- Harman RR, Goddard J, Shivaji R, Cronin JT. 2020 Frequency of occurrence and population-dynamic consequences of different forms of density-dependent emigration. *Am. Nat.* **195**, 851–867. (doi:10.1086/708156)
- Yoder JM, Marshall EA, Swanson DA. 2004 The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behav. Ecol.* **15**, 469–476. (doi:10.1093/beheco/arh037)
- Binning SA, Shaw AK, Roche DG. 2017 Parasites and host performance: incorporating infection into our understanding of animal movement. *Integr. Comp. Biol.* **57**, 267–280. (doi:10.1093/icb/ix024)
- Bonte D *et al.* 2012 Costs of dispersal. *Biol. Rev. Camb. Philos. Soc.* **87**, 290–312. (doi:10.1111/j.1469-185X.2011.00201.x)
- Carbone C, Cowlishaw G, Isaac NJB, Rowcliffe JM. 2005 How far do animals go? Determinants of day range in mammals. *Am. Nat.* **165**, 290–297. (doi:10.1086/426790)
- Haskell JP, Ritchie ME, Olff H. 2002 Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. *Nature* **418**, 527–530. (doi:10.1038/nature00840)
- Wootton JT, Emmerson M. 2005 Measurement of interaction strength in nature. *Annu. Rev. Ecol. Evol. Syst.* **36**, 419–444. (doi:10.1146/annurev.ecolsys.36.091704.175535)
- Preisser EL, Bolnick DI, Benard MF. 2005 Scared to death? The effects of intimidation and consumption in predator–prey interactions. *Ecology* **86**, 501–509. (doi:10.1890/04-0719)
- Strauss AT, Civitello DJ, Cáceres CE, Hall SR. 2015 Success, failure and ambiguity of the dilution effect among competitors. *Ecol. Lett.* **18**, 916–926. (doi:10.1111/ele.12468)
- Goodacre SL, Martin OY, Bonte D, Hutchings L, Woolley C, Ibrahim K, Thomas CFG, Hewitt GM. 2009 Microbial modification of host long-distance dispersal capacity. *BMC Biol.* **7**, 32. (doi:10.1186/1741-7007-7-32)
- Moore AT, Brown CR. 2014 Dispersing hemipteran vectors have reduced arbovirus prevalence. *Biol. Lett.* **10**, 20140117. (doi:10.1098/rsbl.2014.0117)
- Moher D, Liberati A, Tetzlaff J, Altman DG, The PRISMA Group. 2009 Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. *PLOS Med.* **6**, e1000097. (doi:10.1371/journal.pmed.1000097)
- O'Dea RE *et al.* 2021 Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biol. Rev. Camb. Philos. Soc.* **96**, 1695–1722. (doi:10.1111/brv.12721)
- Lajeunesse MJ. 2016 Facilitating systematic reviews, data extraction and meta-analysis with the METAGEAR package for R. *Methods Ecol. Evol.* **7**, 323–330. (doi:10.1111/2041-210X.12472)
- Landis JR, Koch GG. 1977 The measurement of observer agreement for categorical data. *Biometrics* **33**, 159–174. (doi:10.2307/2529310)
- Lajeunesse M. 2021 juicr: Automated and Manual Extraction of Numerical Data from Scientific Images. See <http://lajeunesse.myweb.usf.edu/> <https://github.com/mjlajeunesse/>.
- Lüdtke D. 2019 esc: Effect Size Computation for Meta Analysis. *Zenodo*. (doi:10.5281/zenodo.1249218)
- Ben-Shachar M, Lüdtke D, Makowski D. 2020 effectsz: Estimation of Effect Size Indices and Standardized Parameters. *J.O.S.S.* **5**, 2815. (doi:10.21105/joss.02815)
- Borenstein M (ed). 2009 *Introduction to meta-analysis*. Chichester, UK: John Wiley & Sons.
- Higgins J, Thomas J, Chandler J, Cumpston M, Li T, Page M, Welch V (eds). 2022 *Cochrane handbook for systematic reviews of interventions*. See <https://training.cochrane.org/handbook/current.ver.6.3>.

39. Wan X, Wang W, Liu J, Tong T. 2014 Estimating the sample mean and standard deviation from the sample size, median, range and/or interquartile range. *BMC Med. Res. Methodol.* **14**, 135. (doi:10.1186/1471-2288-14-135)
40. Koricheva J, Gurevitch J, Mengersen K (eds). 2013 *Handbook of meta-analysis in Ecology and evolution*. Princeton, NJ: Princeton University Press. (doi:10.1515/9781400846184)
41. Tomczak M, Tomczak E. 2014 The need to report effect size estimates revisited. An overview of some recommended measures of effect size. *Trends Sport Sci.* **1**, 19–25.
42. Correll J, Mellinger C, Pedersen EJ. 2022 Flexible approaches for estimating partial eta squared in mixed-effects models with crossed random factors. *Behav. Res. Methods* **54**, 1626–1642. (doi:10.3758/s13428-021-01687-2)
43. Lakens D. 2013 Calculating and reporting effect sizes to facilitate cumulative science: a practical primer for *t*-tests and ANOVAs. *Front. Psychol.* **4**, 863. (doi:10.3389/fpsyg.2013.00863)
44. Auger G, Pottier J, Mathieu J, Jabot F. 2024 Space use of invertebrates in terrestrial habitats: Phylogenetic, functional and environmental drivers of interspecific variations. *Glob. Ecol. Biogeogr.* **33**, e13811. (doi:10.1111/geb.13811)
45. Broekman MJE, Hoeks S, Freriks R, Langendoen MM, Runge KM, Savenco E, ter Harmsel R, Huijbregts MAJ, Tucker MA. 2023 HomeRange: a global database of mammalian home ranges. *Global Ecol. Biogeogr.* **32**, 198–205. (doi:10.1111/geb.13625)
46. Tamburello N, Côté IM, Dulvy NK. 2015 Energy and the scaling of animal space use. *Am. Nat.* **186**, 196–211. (doi:10.1086/682070)
47. Tucker MA, Ord TJ, Rogers TL. 2014 Evolutionary predictors of mammalian home range size: body mass, diet and the environment. *Glob. Ecol. Biogeogr.* **23**, 1105–1114. (doi:10.1111/geb.12194)
48. Pinsky M, McCauley D. 2019 *Home range and body size data compiled from the literature for marine and terrestrial vertebrates*. (doi:10.1575/1912/bco-dmo.752795.1)
49. Chamberlain SA, Bronstein JL, Rudgers JA. 2014 How context dependent are species interactions? *Ecol. Lett.* **17**, 881–890. (doi:10.1111/ele.12279)
50. Grafen A. 1989 The phylogenetic regression. *Phil. Trans. R. Soc. Lond. B.* **326**, 119–157. (doi:10.1098/rstb.1989.0106)
51. Paradis E, Schliep K. 2019 ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528. (doi:10.1093/bioinformatics/bty633)
52. Viechtbauer W. 2010 Conducting meta-analyses in R with the metafor package. *J. Stat. Softw.* **36**, 1–48. (doi:10.18637/jss.v036.i03)
53. R Core Team. 2023 R: A Language and Environment for Statistical Computing. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
54. Bartoń K. 2023 MuMIn: Multi-Model Inference. See <https://CRAN.R-project.org/package=MuMIn>.
55. Rosenberg MS. 2005 The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution* **59**, 464–468. (doi:10.1111/j.0014-3820.2005.tb01004.x)
56. Egger M, Davey Smith G, Schneider M, Minder C. 1997 Bias in meta-analysis detected by a simple, graphical test. *BMJ* **315**, 629–634. (doi:10.1136/bmj.315.7109.629)
57. Nakagawa S, Santos ESA. 2012 Methodological issues and advances in biological meta-analysis. *Evol. Ecol.* **26**, 1253–1274. (doi:10.1007/s10682-012-9555-5)
58. Lenth R. 2023 *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version. See <https://CRAN.R-project.org/package=emmeans> vers. 1.8.8.
59. Rosenthal MF, Gertler M, Hamilton AD, Prasad S, Andrade MCB. 2017 Taxonomic bias in animal behaviour publications. *Anim. Behav.* **127**, 83–89. (doi:10.1016/j.anbehav.2017.02.017)
60. Bánki O *et al.* 2023 *Catalogue of life checklist*. (doi:10.48580/dfgnm)
61. Senior AM, Grueber CE, Kamiya T, Lagisz M, O'Dwyer K, Santos ESA, Nakagawa S. 2016 Heterogeneity in ecological and evolutionary meta-analyses: its magnitude and implications. *Ecology* **97**, 3293–3299. (doi:10.1002/ecy.1591)
62. Lowe WH, McPeck MA. 2014 Is dispersal neutral? *Trends Ecol. Evol.* **29**, 444–450. (doi:10.1016/j.tree.2014.05.009)
63. Matthysen E. 2005 Density-dependent dispersal in birds and mammals. *Ecography* **28**, 403–416. (doi:10.1111/j.0906-7590.2005.04073.x)
64. Cote J, Bestion E, Jacob S, Travis J, Legrand D, Baguette M. 2017 Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography* **40**, 56–73. (doi:10.1111/ecog.02538)
65. Holt RD, Barfield M. 2008 Habitat selection and niche conservatism. *Isr. J. Ecol. Evol.* **54**, 295–309. (doi:10.1560/IJEE.54.3-4.295)
66. Ravigné V, Dieckmann U, Olivieri I. 2009 Live where you thrive: joint evolution of habitat choice and local adaptation facilitates specialization and promotes diversity. *Am. Nat.* **174**, E141–E169. (doi:10.1086/605369)
67. Weisser WW. 2001 The effects of Predation on dispersal. In *Dispersal* (eds J Clobert, E Danchin, AA Dhondt, JD Nichols), pp. 180–188. Oxford, UK: Oxford University Press. (doi:10.1093/oso/9780198506607.001.0001)
68. Thierry M, Cote J, Bestion E, Legrand D, Clobert J, Jacob S. 2024 The interplay between abiotic and biotic factors on dispersal decisions in metacommunities. *Phil. Trans. R. Soc. B.* **379**, 20230137. (doi:10.1098/rstb.2023.0137)
69. Baines CB, McCauley SJ, Rowe L. 2014 The interactive effects of competition and predation risk on dispersal in an insect. *Biol. Lett.* **10**, 20140287. (doi:10.1098/rsbl.2014.0287)
70. Hammill E, Fitzjohn RG, Srivastava DS. 2015 Conspecific density modulates the effect of predation on dispersal rates. *Oecologia* **178**, 1149–1158. (doi:10.1007/s00442-015-3303-9)
71. Ventura L, Smith DR, Lubin Y. 2017 Crowding leads to fitness benefits and reduced dispersal in a colonial spider. *Behav. Ecol.* **28**, 1384–1392. (doi:10.1093/beheco/arx106)
72. Sloggett JJ, Weisser WW. 2002 Parasitoids induce production of the dispersal morph of the pea aphid, *Acyrtosiphon pisum*. *Oikos* **98**, 323–333. (doi:10.1034/j.1600-0706.2002.980213.x)
73. Tremmel M, Steinitz H, Kliot A, Harari A, Lubin Y. 2020 Dispersal, endosymbiont abundance and fitness-related consequences of inbreeding and outbreeding in a social beetle. *Biol. J. Linn. Soc.* **129**, 717–727. (doi:10.1093/biolinnean/blz204)
74. Nørgaard LS, Zilio G, Saade C, Gougat-Barbera C, Hall MD, Fronhofer EA, Kaltz O. 2021 An evolutionary trade-off between parasite virulence and dispersal at experimental invasion fronts. *Ecol. Lett.* **24**, 739–750. (doi:10.1111/ele.13692)
75. Holomuzki JR, Pillsbury RW, Khandwala SB. 1999 Interplay between dispersal determinants of larval hydropsychid caddisflies. *Can. J. Fish. Aquat. Sci.* **56**, 2041–2050. (doi:10.1139/f99-141)
76. Kaster JL. 1989 Observations of predator-prey interaction on dispersal of an oligochaete prey, *Limnodrilus hoffmeisteri*. *Hydrobiologia* **180**, 191–193. (doi:10.1007/BF00027552)
77. Reim E, Baguette M, Günter F, Fischer K. 2018 Emigration propensity and flight performance are decoupled in a butterfly. *Ecosphere* **9**, e02502. (doi:10.1002/ecs2.2502)
78. Achiano KA, Giliomee JH. 2008 Food-, temperature- and crowding-mediated laboratory dispersal of *Carcinops pumilio* (Erichson) (Coleoptera: Histeridae), a predator of house fly (Diptera: Muscidae) eggs and larvae. *Afr. Entomol.* **16**, 115–121. (doi:10.4001/1021-3589-16.1.115)
79. Matthysen E. 2012 Multicausality of dispersal: a review. In *Dispersal Ecology and evolution* (eds J Clobert, M Baguette, TG Benton, JM Bullock), pp. 3–18. Oxford, UK: Oxford University Press. (doi:10.1093/acprof:oso/9780199608898.001.0001)
80. Schmitz OJ, Miller JRB, Trainor AM, Abrahms B. 2017 Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. *Ecology* **98**, 2281–2292. (doi:10.1002/ecy.1916)

81. Miyasaka H, Nakano S. 2001 Drift dispersal of mayfly nymphs in the presence of chemical and visual cues from diurnal drift- and nocturnal benthic-foraging fishes. *Freshw. Biol.* **46**, 1229–1237. (doi:10.1046/j.1365-2427.2001.00745.x)
82. Wooster D, Sih A. 1995 A review of the drift and activity responses of stream prey to predator presence. *Oikos* **73**, 3–8. (doi:10.2307/3545718)
83. Baines CB, Diab S, McCauley SJ. 2020 Parasitism risk and infection alter host dispersal. *Am. Nat.* **196**, 119–131. (doi:10.1086/709163)
84. Zelnik YR, Barbier M, Shanafelt DW, Loreau M, Germain RM. 2024 Linking intrinsic scales of ecological processes to characteristic scales of Biodiversity and functioning patterns. *Oikos* e10514. (doi:10.1111/oik.10514)
85. Hunt JJFG, Bonsall MB. 2009 The effects of colonization, extinction and competition on co-existence in metacommunities. *J. Anim. Ecol.* **78**, 866–879. (doi:10.1111/j.1365-2656.2009.01532.x)
86. Selonen V, Fey K, Hämäläinen S, Turkia T, Korpimäki E. 2018 Do predators modify context-dependent dispersal of red squirrels? *Behav. Ecol. Sociobiol.* **72**, 136. (doi:10.1007/s00265-018-2554-y)
87. Selonen V, Wistbacka R, Korpimäki E. 2016 Food abundance and weather modify reproduction of two arboreal squirrel species. *J. Mammal.* **97**, 1376–1384. (doi:10.1093/jmammal/gyw096)
88. Selonen V, Wistbacka R. 2016 Siberian flying squirrels do not anticipate future resource abundance. *BMC Ecol.* **16**, 51. (doi:10.1186/s12898-016-0107-7)
89. Cote J *et al.* 2022 Dispersal syndromes in challenging environments: a cross-species experiment. *Ecol. Lett.* **25**, 2675–2687. (doi:10.1111/ele.14124)
90. Cote J, Fogarty S, Tymen B, Sih A, Brodin T. 2013 Personality-dependent dispersal cancelled under predation risk. *Proc. R. Soc. B* **280**, 20132349. (doi:10.1098/rspb.2013.2349)
91. Debeffe L, Morellet N, Verheyden-Tixier H, Hoste H, Gaillard J, Cargnelutti B, Picot D, Sevilá J, Hewison AJM. 2014 Parasite abundance contributes to condition-dependent dispersal in a wild population of large herbivore. *Oikos* **123**, 1121–1125. (doi:10.1111/oik.01396)
92. Bestion E, Teyssier A, Aubret F, Clobert J, Cote J. 2014 Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. *Proc. R. Soc. B* **281**, 20140701. (doi:10.1098/rspb.2014.0701)
93. Terui A, Ooue K, Urabe H, Nakamura F. 2017 Parasite infection induces size-dependent host dispersal: consequences for parasite persistence. *Proc. R. Soc. B* **284**, 20171491. (doi:10.1098/rspb.2017.1491)
94. Baines CB, McCauley SJ, Rowe L. 2015 Dispersal depends on body condition and predation risk in the semi-aquatic insect, *Notonecta undulata*. *Ecol. Evol.* **5**, 2307–2316. (doi:10.1002/ece3.1508)
95. Bonte D, Dähirel M. 2017 Dispersal: a central and independent trait in life history. *Oikos* **126**, 472–479. (doi:10.1111/oik.03801)
96. Bestion E, Legrand D, Baines CB, Bonte D, Coulon A, Dähirel M *et al.* 2024 Data from Species interactions affect dispersal: a meta-analysis. Figshare. (doi:10.6084/m9.figshare.25887136)