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ANIMAL DISPERSAL COSTS ARE NOT UNIVERSAL

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ABSTRACT Dispersal is a keystone process shaping ecological and evolutionary dynamics, often assumed to be inherently costly. We synthesized 717 effect sizes from 210 studies across 150 animal species, spanning all continents and ecosystems, to test this assumption. Contrary to long-standing dogma, we found no overall effect of dispersal on fitness (mean effect size: -0.02, 95% CIs: -0.08 to 0.03). No tested biological or methodological moderators explained this variation. Instead, heterogeneity was highest within studies, suggesting that dispersal is highly context-dependent within studies and species. These findings align with game-theoretic expectations that dispersal and philopatry are alternative strategies maintained by balancing or frequency-dependent selection. Our findings are consistent with the view that dispersal involves a balancing act between strategies that yield equivalent long-term payoffs across variable conditions.

Dispersal has long occupied a paradoxical place in evolutionary ecology (*1*). On one hand, it is essential for gene flow, species persistence, and colonization (*2*). On the other, it is frequently assumed to exact steep fitness costs (*3*). Classic models have portrayed dispersal as a "suicidal venture" (*4*), where individual animals pay for movement through elevated risks, energetic demands, and lost opportunities (*5*–*10*). This framing, deeply embedded in the literature, has shaped decades of empirical and theoretical work (*11*–*15*). Yet dispersal persists across taxa and time, suggesting that it must also confer fitness benefits (*16*–*19*). Evolutionary theory predicts that costly behaviours should not endure unless they are balanced by returns - whether direct, delayed, or context-dependent (*20*). This logic is consistent with classic island biogeography and metapopulation perspectives, where dispersal is maintained when connectivity yields net fitness returns, but can be reduced or lost when costs are no longer offset (*21*–*23*). Indeed, empirical studies increasingly report benefits to dispersers (*16*, *24*, *25*), hinting that dispersal and philopatry may coexist as alternative strategies (*26*–*28*).

This ecological and evolutionary tension, between the assumed costs and the persistence of dispersal, raises a central question: is dispersal generally penalized? Resolving this is key to understanding how dispersal strategies evolve and how populations will respond to a rapidly changing world (*29*–*37*). Yet, despite decades of debate, no synthesis has systematically tested whether dispersal is, in fact, consistently costly across species, contexts, and fitness components.

GLOBAL SYNTHESIS OF DISPERSAL AND FITNESS RELATIONSHIPS

To test the generality of dispersal costs, we synthesized data from 210 studies, encompassing 717 effect sizes across 150 animal species and six major taxonomic groups. Most studies were on birds (50%) or mammals (43%), and the remaining 7% included reptiles, fish, insects, and arachnids (Fig. 1A). These

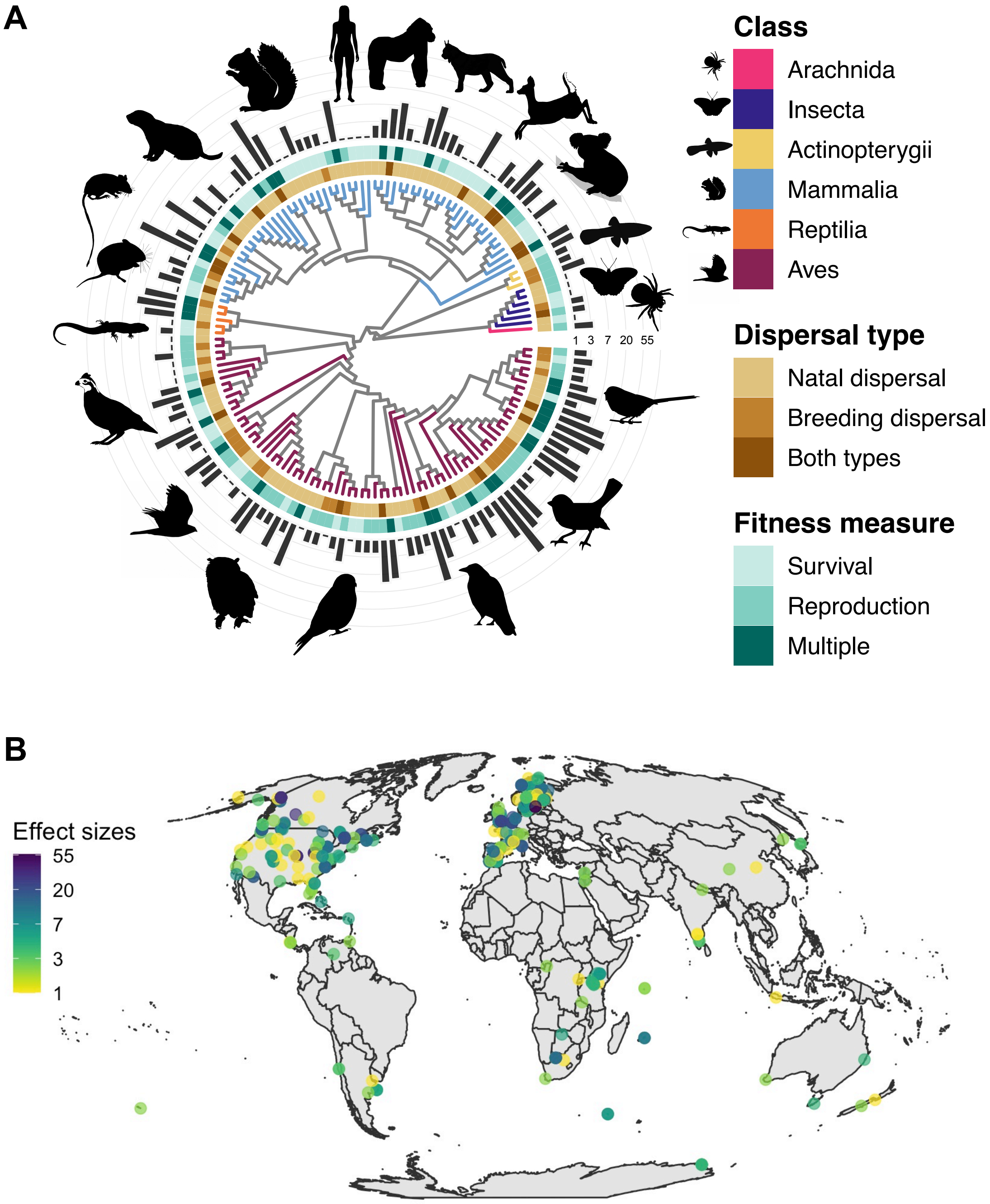

FIG. 1. (A) Phylogenetic distribution of species in the meta-analysis. The total number of effect sizes (outside ring numbers and bars in black) for 148 species are shown alongside dispersal type (innermost ring - natal: movement between birth site and the first breeding site; breeding dispersal: movement between consecutive breeding sites) and fitness measure for survival, reproduction, or both survival and reproduction (multiple) across taxonomic classes (middle ring). We show animal silhouettes from representative classes within each taxonomic group when possible (sources acknowledged here:
https://www.phylopic.org/permalinks/e95fe5832e575cbcff7c8fe66ad2d816d45593904a733d36ce367adaad8cdd7d).
(B) Global distribution of all studies in our meta-analysis of animal dispersal fitness costs. The total number of effect sizes is represented as colored dots and is assigned to the study location.

studies span three centuries (1720-2022), all continents, and terrestrial and aquatic systems, providing the most comprehensive assessments of dispersal consequences to date (Fig. 1B). As in other large-scale syntheses (*38*), our data are geographically biased toward temperate regions. We distinguished between natal dispersal (movement from birthplace to first breeding site) and breeding dispersal (movement between breeding attempts) (*39*). Fitness outcomes were primarily measured through reproduction and survival, which are direct determinants of individual and population performance. Effect sizes were expressed as Fisher's Z-transformed correlations (Zr), derived from either standardized contrasts between dispersers and non-dispersers or from correlations between dispersal distance and fitness. To aid interpretation, positive effect sizes indicate that dispersers had higher fitness than non-dispersers and negative effect sizes indicate dispersers had lower fitness than non-dispersers. Taken together, this body of literature provided an opportunity to evaluate whether the widely assumed costs of dispersal emerge consistently across ecological and methodological contexts.

DISPERSAL IS NOT UNIVERSALLY COSTLY

The distribution of dispersal effects on fitness - with an average close to zero - was remarkably consistent across taxa, sexes, fitness measures, or other aspects of methodology (Fig. 2; Fig. 3). Out of the 210 studies, 151 studies stated an assumption about dispersal's fitness consequences; nearly half (48%) predicted it to be disadvantageous, 42% recognized that there could be both costs and benefits, and only 10% indicated it was expected to be beneficial (Fig. 3H). Yet, across all effect sizes, the mean dispersal effect was indistinguishable from zero (Zr = -0.02; 95% CI: -0.08 to 0.03), and 95% of effect sizes fell between -0.68 and 0.63 (prediction intervals). Dispersers were neither generally penalized nor rewarded. This result was robust to possible publication bias, small-study bias, and to potentially overwhelming effects of single studies or species (Fig. S26-S32 on the dedicated repository https://martinig.github.io/Fitness-and-dispersal-MA/). The mismatch between the common expectation of dispersal being disadvantageous raises questions about the generality of classic models that predict steep, universal realized fitness costs of dispersal. While such models may apply to all dispersers, most empirical studies necessarily focus on survivors. As a result, long-standing assumptions about costly dispersal may reflect tradition and theoretical precedent more than a broad empirical pattern or realized fitness outcomes (*3*).

DISPERSAL OUTCOMES VARY IDIOSYNCRATICALLY AMONG SPECIES

Only rare exceptions to the overall neutral effect of dispersal emerged. For example, ruffed grouse (*Bonasa umbellus*) showed an overall positive dispersal effect (Zr = 0.27; 95% CI: 0.05 to 0.50; *n* = 3 effect sizes from 1 study), whereas Tasmanian nativehens (*Gallinula mortierii*; Zr = -0.23; 95% CI: -0.45 to -0.001; *n* = 4 effect sizes from 1 study) and cougars (*Puma concolor*; Zr = -0.40; 95% CI: -0.64 to -0.16; *n* = 1 effect sizes from 1 study) showed negative effects (Fig. S25 on the dedicated repository https://martinig.github.io/Fitness-and-dispersal-MA/). However, such cases were rare and came from individual studies. No higher taxonomic class, including birds and mammals, which dominated the dataset (Fig. 1A), showed consistent positive or negative dispersal effects (Fig. 2B).

Neither dispersal duration, timing of fitness measurement (prospection versus settlement), dispersal type (natal versus breeding), nor individual characteristics (sex, generation, or life stage) explained the heterogeneity of effects (Fig. 2 and Fig. 3). We predicted that juveniles prospecting during natal dispersal would entail greater fitness costs, and that shorter dispersal durations would show more variability due to acute environmental

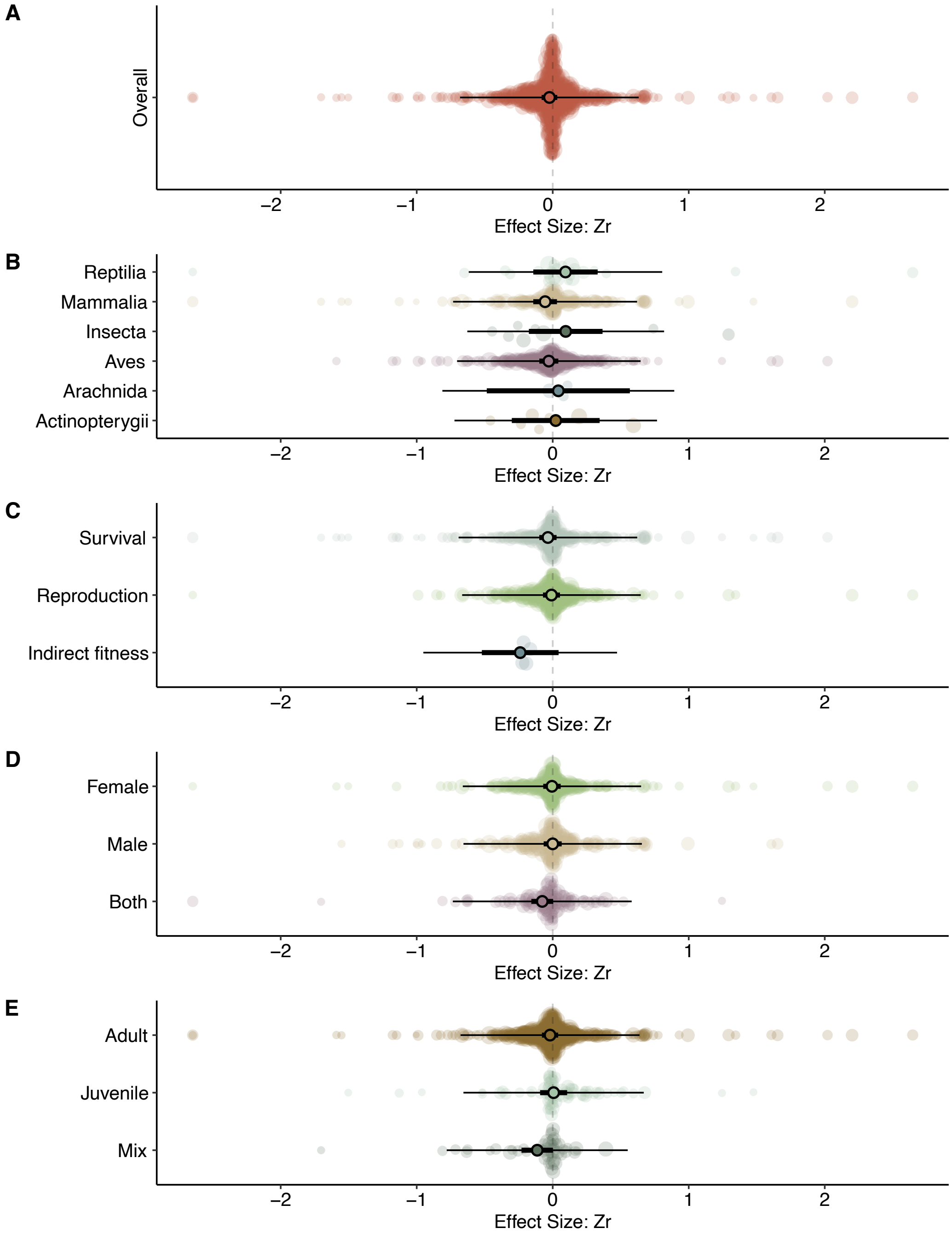

FIG. 2. Mean fitness effects of all investigated moderators from uni-moderator meta-regression models. We present mean effect sizes (Zr) along with 95% confidence (thicker bar) and prediction (thinner bars) intervals are depicted along with individual data points (semi-transparent circles) with size scaled by precision (1/SE). Overall effect size (**A**) and moderators: (**B**) taxonomic classes: Birds (50%) and mammals (43%) made up the majority of the data, followed by reptiles (3%), insects (2%), fish (1%), and spiders (<1%). **(C)** Fitness measure: Most effect sizes came from measures of reproduction (53%) and survival (46%), with indirect fitness contributing less than 1% of the data. (**D**) Sex: Studies commonly reported sex-specific effects, with 46% of effect sizes coming from females, 36% from males, and 18% combining sexes. (**E**) Life history stage: Most studies focused on adults and yearlings ("Adults"; 82% of effect sizes), with fewer examining juveniles (12%) or mixed-age groups (6%). We report the number of effect sizes and number of studies for all moderators (Fig. S2-S18 on the dedicated repository https://martinig.github.io/Fitness-and-dispersal-MA/).

mismatches. However, these expectations were not supported (Fig. 2 and Fig. 3). A few weak patterns did emerge, such as in studies combining female and male mammals (Zr = -0.18; 95% CI: -0.30 to -0.05; Table S16 on the dedicated repository https://martinig.github.io/Fitness-and-dispersal-MA/). Yet, studies explicitly testing the fitness effects of dispersal, or those that assumed dispersal would be costly or beneficial, showed no consistent effect (Fig. 3G-H). Together, these findings challenge the view that dispersal is inherently detrimental, alongside the view that there are any clear, measurable and universal benefits.

DISPERSAL OUTCOMES REFLECT LOCAL AND TEMPORAL HETEROGENEITY

Most of the variation in dispersal outcomes was not explained by species-level differences, taxonomic grouping, or any tested moderator. Instead, heterogeneity was high (I^2 = 97.0%) and overwhelmingly (64.1%) attributed to within-study variation (i.e., residuals), rather than to species (14.6%) or study (18.3%). Phylogeny explained none of this variation (0.00%). These results align with theory predicting that dispersal outcomes are tightly coupled to spatial and temporal heterogeneity in selection pressures (*40*). Within studies, fitness measures - whether eggs laid, hatched, or fledged - are inherently dynamic and influenced by short- and long-term environmental fluctuations. Environmental fluctuations, such as resource abundance or population density, likely make dispersal beneficial for some fitness components in some years or locations and costly for others (*41*, *42*).

This context dependence is particularly relevant in species like ruffed grouse, Tasmanian native hens, and cougars, where directional selection may exist (this study), but where data remain sparse. When data from multiple years or sites are aggregated, these opposing effects may appear to “cancel out”, contributing to the net-neutral effects observed here. These patterns echo the “paradox of stasis”, where traits subject to apparent directional selection exhibit little evolutionary change over time, suggesting fluctuating selection, undetected stabilizing selection, or both (*43*–*45*). Importantly, shifting ecological conditions may tip the balance towards or against dispersal at particular times and places (*46*). The high within-study variation we detected is consistent with this view, suggesting that populations maintain a portfolio of dispersal strategies that can be flexibly deployed as circumstances dictate (*47*). Without accounting for this context-dependent variation, studies may miss crucial insights into the ecological mechanisms driving dispersal and its fitness consequences.

These shifting landscapes create conditions in which no single strategy consistently outperforms another. These patterns align with expectations from game theory, which would predict that dispersal and philopatry can coexist as alternative strategies maintained by frequency-dependent selection (*20*). Neither tactic is inherently superior; instead, their relative fitness depends on their frequency in the population and the behaviors of other individuals (*48*, *49*). Such variation likely selects for plastic or condition-dependent dispersal strategies, maintaining both dispersers and non-dispersers within populations (*50*–*52*). Our findings are consistent with this view: far from maladaptive, dispersal is a context-dependent tactic that balances the scales of fitness across time and space.

INVISIBLE LOSSES AND THE CHALLENGE OF MEASURING DISPERSAL OUTCOMES

A persistent limitation in dispersal research is that unsuccessful dispersers often go undetected, biasing fitness estimates toward survivors. This viability selection filters out individuals who fail to settle or reproduce, obscuring the true distribution of dispersal outcomes (*53*). As a result, dispersal studies may underestimate the frequency or magnitude of dispersal costs by conflating dispersal with dispersal success (*54*).

Misclassifications further compound this issue, particularly in breeding dispersal, where individuals are often labelled as philopatric based on one season of residency, despite prior dispersal. Stricter definitions, such as those proposed by Récapet et al. (*55*), and longitudinal tracking, can reduce this bias, but few studies currently meet this standard. This limitation could contribute to the apparent neutrality of dispersal effects in our synthesis, either by reflecting genuinely balanced net fitness outcomes or by failing to isolate costs incurred specifically during movement itself (e.g., physiological or energetic expenditure), as well as by concealing costs that are filtered out prior to measurement (e.g., mortality, failed dispersers, or condition-dependent dispersal (*56*, *57*)). Condition-dependent dispersal is one potential compensatory mechanism; however, among the 60 studies that explicitly examined it, results

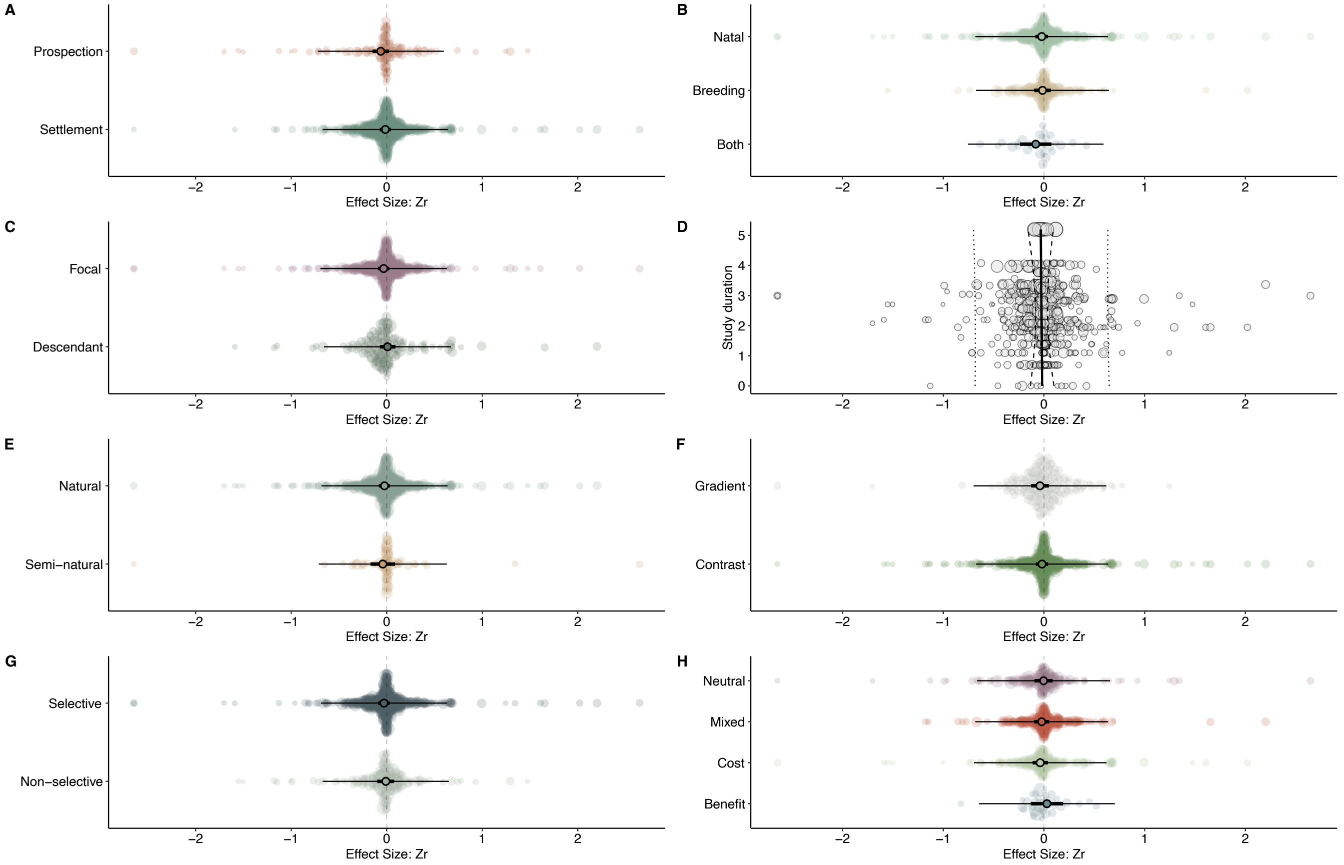

FIG. 3. Mean fitness effects of all investigated moderators from uni-moderator meta-regression models. We present mean effect sizes (Zr) along with 95% confidence (thicker bar) and prediction (thinner bars) intervals are depicted along with individual data points (semi-transparent circles) with size scaled by precision (1/SE). (**A**) Dispersal type: Natal dispersal was studied more frequently (70%) than breeding dispersal (26%), while 4% of studies did not distinguish between dispersal type. (**B**) Dispersal phase: Settlement (82%) was studied more than prospection (18%). (**C**) Generation: The majority of the data (84%) came from the dispersers themselves rather than their descendants (16%). (**D**) Study duration (log years). (**E**) Study design: The majority of effect sizes came from unmanipulated, wild populations (90%), while 10% came from semi-natural (i.e., experimental) studies. (**F**) Comparison type: Most studies reported effect sizes from systems that contrasted dispersers with non-dispersers (77%) rather than continuous dispersal gradients (23%). (**G**) Selective reporting (i.e., if fitness was the main focus of the study): 77% of effect sizes came from studies that were explicitly interested in the fitness effects of dispersal, while 23% came from studies were this was not the case. (**H**) Assumptions made about dispersal: 25% of effect sizes came from studies were there was no assumption made about dispersal, leaving 151 studies that made an assumption; of these 151 studies, 42% came from studies that assumed both costs and benefits, 48% from studies assuming only costs, and 10% from studies that assumed only benefits. We report the number of effect sizes and number of studies for all moderators (Fig. S2-S18 on the dedicated repository https://martinig.github.io/Fitness-and-dispersal-MA/).

were mixed, with over half reporting no detectable effect on dispersal outcomes.

Dispersal may also carry fitness consequences across generations, influencing the reproductive success of descendants. This is because the fitness consequences of dispersal are unlikely to manifest fully within a single generation, but instead emerge as the combined result of an individual's fitness and that of its descendants over time (*58*). Yet, such multigenerational effects were rarely captured in the literature (*16*, *59–61*), despite being critical for understanding the evolutionary dynamics of dispersal. Together, these limitations highlight that observed fitness outcomes cannot be straightforwardly mapped onto the causal processes governing dispersal.

TOWARDS RESOLVING DISPERSAL'S EVOLUTIONARY PUZZLE

Despite its many complexities, dispersal endures because it works. It is neither universally costly nor consistently beneficial in terms of realized fitness outcomes. Instead, its fitness consequences are highly variable, shaped by local ecological and demographic contexts rather than by species identity or life history. This variability likely reflects an evolutionary equilibrium, where dispersal and philopatry persist as alternative strategies under frequency-dependent selection and environmental heterogeneity.

This balancing act raises a fundamental evolutionary question: does dispersal operate as an alternative strategy determined by genetic polymorphism, as a probabilistic mix of tactics in a genetically monomorphic population, or a conditional strategy based on status or context (*13*, *50–52*, *60*, *62*, *63*)? Dispersers and non-dispersers often differ in behavior, physiology, morphology, and life history (*12*, *64–67*), suggesting dispersal is not merely a constraint, but an alternative strategy shaped by fluctuating environments (*16*, *48*, *49*, *68*, *69*). Territory quality, social structure, local density, and sex-biased dispersal have all been implicated in shaping dispersal and its consequences for reproduction (*11*, *17*, *68*, *70–79*). In many cases, dispersal may be the only viable route to reproductive opportunity, particularly when faced with habitat saturation or the risk of inbreeding (*80*, *81*).

The challenge ahead is not to determine whether dispersal has consequences, but to understand when, for whom, and under what conditions it does. Dispersal is best understood not through a single evolutionary lens, but as a flexible strategy shaped by shifting ecological and social pressures. Resolving how these payoffs are generated, maintained, and altered by environmental change will require integrative approaches that connect behavioural mechanisms to fitness outcomes across space and time.

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DATA ACCESSIBILITY STATEMENT

All data, code, and materials are available online (https://github.com/martinig/Fitness-and-dispersal-MA), and they will be archived in a public repository after the manuscript has been accepted for publication.

AUTHOR CONTRIBUTION STATEMENT

Conceptualization: ARM; Methodology: ARM, ML, & SN; Investigation: ARM, SLPB, ML, YY, & SN; Visualization: ARM; Writing – original draft: ARM; Writing – review & editing: ARM, SLPB, ML, & SN.

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